

# Pinniped Phylogeny

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**ABSTRACT.**—In our view, presentations inferring pinniped diphyly provide inadequate evidence of "otarioid" monophyly and inadequate evidence that phocids are related to some nonpinniped group. The integrated assessment of higher-level pinniped relationships presented here, based on cranial, postcranial, and soft-anatomical characters from most living and adequately known fossil pinnipeds, supports pinniped monophyly. We scored more than 150 character transformations on a generic-level character matrix and used a computer parsimony algorithm (PAUP) to construct a maximally parsimonious phylogenetic hypothesis for the group. Its major outlines are as follows: (*Enaliarctos* (*Pteronarctos* (Otaridae (Odobenidae (*Pinnarctidion*, *Desmatophoca*, *Allodesmus* (Phocidae)))))). Internally, the data are highly consistent. Convergence is much less pervasive than generally assumed, with reversals being the dominant pattern of homoplasy.

## INTRODUCTION

Few mammalian examples more forcefully illustrate the impact of phylogenetic systematic methods on notions of a particular group's evolutionary history than does the case of the pinnipeds. Recent cladistic studies have addressed questions of relationships within the otariids (fur seals and sea lions) (Berta and Deméré 1986) and phocids (true seals) (Muizon 1982a; Wyss 1988b), odobenid (walrus) affinities (Wyss 1987), and the placement of certain archaic fossil taxa (Wyss 1987; Berta et al. 1989; Berta 1991). The net result of these efforts is a concept of pinniped relationships drastically different from what was generally accepted until relatively recently. We outline here the novel aspects of these recent proposals and present their methodological basis. In addition to providing new information on the distribution of morphological characters, we combine and revise the data sets of these previous studies in an attempt to synthesize what we regard to be the currently best supported hypothesis of pinniped relationships. We present the evidence for this hypothesis in the form of a taxon-character matrix in hopes that it may serve as a starting point for future phylogenetic analyses of pinnipeds. If this matrix generates debate about character coding, or discussion over the in- or exclusion of certain characters in the analysis, or if it inspires the examination and description of additional characters that either support or refute the relationships we favor, in short, if it evolves, it will have served its purpose.

## HISTORICAL CONSIDERATIONS

All recent workers agree that pinnipeds are members of a carnivoran subclade, the Arctoidea, that includes among terrestrial lineages mustelids, ursids, and procyonids (Tedford 1976). Controversy about relationships among the major groups of pinnipeds centers on the relationship of phocids to the rest of the Arctoidea. This disagreement reduces to two fundamental questions of monophyly. Before we consider these (to eliminate possible ambiguity) we must define our usage of "monophyly." We use the term (sensu Hennig 1966) to denote a group of taxa derived from a common ancestor and including all of the descendants of that common ancestor. Evidence for monophyly of a particular group consists of the shared possession of evolutionary novelties (synapomorphies) by its members. The two central questions concerning the phylogenetics of "fin-footed" arctoids are (1) is the group as a whole descended from an exclusive common ancestor? (i.e., are pinnipeds monophyletic?) and (2) do pinnipeds excluding phocids have a common ancestor not also shared by phocids? (i.e., are the Otarioidea, defined as the Otariidae and Odobenidae plus certain extinct forms, monophyletic?) (Fig. 1).

The question of single versus multiple origin(s) dates from Mivart's (1885) suggestion that the group's origin was likely compound, with sea lions and walrus derived from ursids and true seals derived from mustelids, otters in particular (Fig. 1B). Although this view was dismissed by several workers over the next half century (e.g., Weber 1904; Gregory 1910), it was not discounted altogether by others (e.g., Kellogg 1922; Howell 1929; Simpson 1945). Thereafter, the notion of multiple pinniped origins regained wide support in the morphological and paleontological literature (McLaren 1960; Tedford 1976; Muizon 1982a,b), a shift influenced particularly by the detailed descriptions of the fossil taxa *Potamotherium* (Savage 1957) and *Enaliarctos* (Mitchell and Tedford 1973). More recently, one of us argued, on the basis of anatomical criteria, in favor of a return to the single-origin interpretation (Wyss 1987) (Fig. 1A), a conclusion consistent with but independent of certain biomolecular and cytologic results (Fay et al. 1967; Arnason 1986; de Jong 1982, 1986). Several subsequent studies (Flynn et al. 1988; Berta et al. 1989; Wyss 1988, 1989) have yielded additional evidence supporting this conclusion, but it continues to engender debate (Wozencraft 1989; Reppening 1990; Bonner 1990).

The second question concerns the phylogenetic validity of the Otarioidea. Since their recognition as distinct groups of mammals, otariids and odobenids have nearly universally been regarded as being more closely related to each other than either is to some third taxon. The observation that the walrus is in many respects more nearly intermediate between otariids and phocids than had been previously appreciated (Fay et al. 1967) signaled an important break from this view. The argument that odobenids are related more closely related to phocids than to otariids took this suggestion one logical step further (Wyss 1987). This proposed phocid-odobenid linkage opened the broader question of where this pair should be placed relative to the other arctoids. Either a special link between mustelids and phocids (plus now odobenids) could continue to be recognized (rendering the Otarioidea polyphyletic), or the association of phocids and odobenids could be recognized within the context of a monophyletic Pinnipedia (rendering the Otarioidea paraphyletic). Thus the questions of otarioid and pinniped monophyly are to some degree interwoven, yet if care is taken both may be evaluated with considerable independence.

To two phylogenetic questions, are pinnipeds monophyletic and are otarioids monophyletic, there are four alternative pairs of responses. All except one of these have recent historical precedent: affirmative, affirmative (no recent proponents); affirmative, negative (Fig. 1A) (Wyss 1987; Berta et al. 1989; Flynn et al. 1988; Wyss and Flynn 1993); negative, negative (Mitchell and Tedford

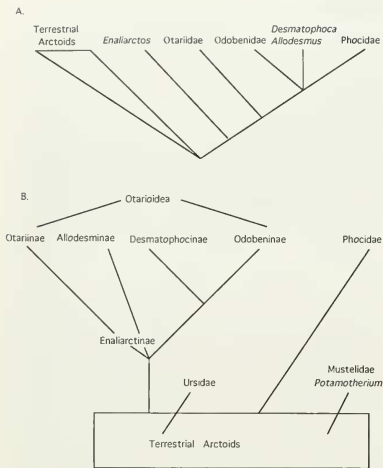


Figure 1. Two competing hypotheses regarding phylogenetic relationships among pinnipeds. A. Current view of pinniped monophyly proposes common ancestry for all pinnipeds from a terrestrial arctoid and supports a sister-group relationship between walruses, seals, and their extinct relatives (Wyss 1987; Berta et al. 1989; Flynn et al. 1988). B. Alternative view of otarioid monophyly proposes independent origins of otarioid and phocid lineages from different terrestrial arctoid groups and supports a sister-group relationship between walruses, sea lions, and their supposed fossil relatives (Barnes 1989, and others).

1973: 205, 278); negative, affirmative (Fig. 1B) (Barnes 1989; Wozencraft 1989; Repenning et al. 1979). We begin with the otarioid question because in some senses it is less complex and easier to address in isolation. We emphasize again that to test the hypothesis of otarioid monophyly apart from the question of pinniped monophyly we must restrict our attention to those derived features characteristic of otarioids not also occurring in phocids.

#### OTARIOID MONOPHYLY

Were pinnipeds demonstrably polyphyletic both the otarioids and phocids could be diagnosed with characters each shares but acquired independently. But because we view otarioid monophyly as a hypothesis in legitimate need of testing we regard claimed otarioid synapomorphies occurring also in phocids as questionable, at least for the initial part of the analysis.

Barnes (1989: fig. 9) presented the most recent, most detailed, and, so far as we are aware, only nominally cladistic diagnosis of the Otarioidea (= his Otariidae). He listed on a branching diagram 20 characters diagnostic of the Otarioidea.

Following the procedure of Wible (1991), we evaluated these 20

features, grouping them as follows: (1) characters for which the reported derived state occurs in relevant outgroups (i.e., nonpinniped Arctoidea) and are therefore primitive and phylogenetically uninformative, (2) characters for which the derived state occurs also in phocids and thus are of uncertain value, (3) characters dubiously described, and (4) characters for which descriptions and distribution are correct but for which we offer comment. Characters are labeled with letters corresponding to the order in which they were listed by Barnes (1989: fig. 9) at node 1, the basal node of his branching diagram.

**Barnes' otarioid "synapomorphies" occurring also in relevant outgroups.**—The derived state of the following characters occurs elsewhere among the Arctoidea and thus represents a level of generality broader than supposed by Barnes (1989).

(a) Neck lengthened. Wyss (1987: 11) discussed previously problems associated with this character. Even if it did characterize otarioids primitively (among odobenids, it doesn't characterize at least *Odobenus*, the only odobenid for which this character can currently be scored), it is not a derived feature among the Carnivora (Bisaillon et al. 1976).

(e) Foramen ovale and posterior opening of alisphenoid canal joined in an elongated recess. The arrangement in ursids is identical (Davis 1964) and almost certainly represents the ancestral condition of the Arctoidea.

(h) Embayment formed in lateral edge of basioccipital loop of median branch of internal carotid artery. This character is well known in ursids (Hunt 1974) and amphyconids (Hunt 1977) and is unquestionably derived at a level broader than the Otarioidea. Although this embayment is absent in all living pinnipeds, in certain phocids (e.g., *Monachus*) sharp crests on the dorsal surface of the basioccipital may represent an osseous vestige of it.

(j) Basal whorl of cochlea directed posteriorly. As discussed by Wyss (1987), this condition characterizes all therian mammals except phocids, which are uniquely specialized in having a more transversely oriented basal whorl.

(l) Auditory ossicles not enlarged. This feature is obviously primitive; the derived condition (ossicles enlarged) originated three times among otarioids according to Barnes' scheme and again (presumably independently) in phocids (see below under Assessing the Pattern of Homoplasy).

(m) Entotympanic restricted to medial part of bulla around carotid canal. This condition corresponds to the type "A" bulla of Hunt (1974), which characterizes ursids, some amphyconids, some mustelids, and perhaps arctoids ancestrally. It is not uniquely diagnostic of otarioids and is therefore not relevant to the question of otarioid monophyly.

(n) Internal acoustic meatus round. A round internal auditory meatus is widespread among terrestrial carnivores and is unquestionably primitive at the level suggested here. The partially or completely divided condition seen in certain "otarioids" and phocids is derived (see discussion of character 24 in analysis below). The meatus is not round in odobenids, *Pinnarctidion*, *Desmatophoca*, or *Alloidesmus*.

(p) Bony tentorium in braincase closely appressed to dorsal surface of eminence containing semicircular canals and floccular fossa. As discussed by Wyss (1987: 24), this is the typical carnivore condition and is undoubtedly primitive. Because the bony tentorium varies widely among the Carnivora (Nojima 1990: table 2) and is difficult to identify, we excluded it from our analysis.

**Barnes' otarioid "synapomorphies" that occur also in phocids.**—The derived state of the following characters occurs also in phocids, a group not included in Barnes' (1989) analysis.

(b) Proximal limb elements shortened. Phocids have previously been recognized as possessing short proximal limb bones (Weber 1904; Howell 1929), and this character has been identified at a

more general level, the Pinnipedimorpha, comprising all pinnipeds plus *Enaliarctos* (Berta et al. 1989).

(c) Maxilla forms part of wall of orbit. Wyss (1987) reported that the derived state in which the maxilla makes a significant contribution to the medial orbital wall and forms the anterior orbital rim also occurs in phocids.

(d) Foramen rotundum and anterior opening of alisphenoid canal combined into one large orbital fissure. Barnes' diagram fails to indicate that *Pinnarctidion* and *Desmatophoca* are exceptions. Phocids also share this derived condition (see discussion of character 19, Appendix 1).

(f) Sphenopalatine foramen enlarged. This derived state also occurs in phocids (see character 12, Appendix 1).

(g) Petrosal isolated from surrounding cranial bones. Repenning (1972) discussed this feature as occurring in phocids also. We have not analyzed it because of the difficulty of quantifying it. We observe only subtle differences in this feature among pinnipeds and terrestrial carnivorous.

(o) Posterior lacerate foramen enlarged, not expanded transversely. The posterior lacerate foramen is enlarged in all phocids as well. In some, however, it is also expanded transversely, but this is apparently a secondary transformation. The condition likely primitive for phocids (e.g., that seen in *Monachus*) is indistinguishable from the supposed "otarioid" condition.

(q) Postglenoid foramen reduced. Phocids are also characterized by having reduced or lost the postglenoid foramen (see character 40, Appendix 1).

(r) Entepicondylar foramen lost from humerus. An entepicondylar foramen is variably present among phocids. From a previous phylogenetic study of the group (Wyss 1988) and our present analysis, presence of this foramen in phocines and most early fossil "monachines" is probably secondary for the group.

(s) Olecranon process of ulna enlarged. As illustrated by Howell (1929: fig. 10), phocids possess a condition of the olecranon process similar to that seen in otariids and odobenids.

*Barnes' (1989) description dubious.*—(k) Head lost from incus. The loss of a head on the incus presupposes that a head was once present, which to us seems highly unlikely. By comparison with the outgroups identified here, the head on the incus is a phocid autapomorphy, absent in all other carnivorous.

*Barnes' (1989) descriptions require modification.*—(i) Mastoid process large and cubic. The size and shape of the mastoid process in nonphocid pinnipeds is not significantly changed over the condition in ursids. Wyss (1987) critiqued the use of this feature at greater length.

(t) Aquatic propulsion by fore- and hindlimbs, principally the forelimbs. Living pinnipeds swim in two different ways. Otariids generate propulsion principally by use of the forelimbs, whereas phocids and odobenids use principally the hindlimbs (English 1976; Gordon 1981, 1983). It has been argued that the ancestor of pinnipeds (or even the ancestor of "otarioids," if this group should prove monophyletic) likely generated propulsion by using all four limbs, as *Enaliarctos* probably did (Berta et al. 1989). This argument applies equally to the ancestor of phocids even if they are not related to other pinnipeds. That some distant ancestor of phocids was a four-limb swimmer is indicated by the phocids' forelimbs' being highly modified (used in steering) despite their propelling themselves by the hindlimbs. If phocids had evolved hindlimb swimming directly from a terrestrial ancestor, the forelimbs should not be as highly transformed as they are.

In summary, Barnes' analysis does little to bolster the case for otarioid monophyly; indeed, it fails to reveal a single persuasive synapomorphy for the group. We recognize that a proposed otarioid synapomorphy is not automatically invalidated by its appearance in phocids. Plausibly, the Phocidae and "Otarioida" could be diag-

nosed with some of the same (convergently acquired) characters, provided that additional characters demonstrated a phylogenetic separation between the two groups.

Historically, the assumed linkage between phocids and mustelids provided this separation, but, as discussed below, recent reviews of characters previously cited in support of this pairing call it into question. The weakness of the evidence supporting the relationship of one pinniped subgroup (phocids) to a terrestrial arctoid lineage (mustelids) to the exclusion of other pinnipeds (a requisite for the acceptance of convergence between otarioids and phocids) leads us to dismiss at least initially apomorphies occurring in both "otarioids" and phocids as necessarily indicating "otarioid" monophyly. Certain "otarioid" synapomorphies might represent convergences; however, we fail to see the logic of accepting this claim in the absence of phylogenetic evidence substantiating a linkage of phocids to some terrestrial lineage of arctoids.

Citing Repenning and Tedford (1977), Wozencraft (1989: 516) argued that there are "many" synapomorphies supporting a walrus-otariid clade, yet he did not list a single shared derived feature in support of this contention. Of the 11 features listed as diagnostic of otarioids in the earlier study, all are primitive or of otherwise unclear phylogenetic significance (Wyss 1987). Thus neither Barnes' nor Wozencraft's analyses identify synapomorphies corroborating otarioid monophyly.

#### PINNIPED MONOPHYLY

Before addressing the question of pinniped monophyly, we first examine the recent arguments in favor of pinniped diphyly. Acceptance of pinniped diphyly requires that two criteria be satisfied: evidence of otarioid monophyly and evidence that phocids are related to some nonpinniped terrestrial group. We concluded in the previous section that otarioid monophyly was not well founded. With respect to the second question, Wyss (1987) reviewed the characters used by Tedford (1976) and Muizon (1982a) to unite phocids and mustelids, concluding that no strong case could be made for a mustelid-phocid pairing. Wozencraft (1989) argued in favor of a mustelid-phocid link but did not discuss the synapomorphies supporting nodes on his maximally parsimonious trees.

To consider all possible pinniped-terrestrial arctoid pairings we include as outgroups the Ursidae, Mustelidae, Procyonidae, and extinct Amphicyonidae. The monophyly of these groups is generally accepted (Flynn et al. 1988). Principal references for these taxa are as follows: Amphicyonidae, Hunt (1974), Hough (1948); Ursidae, Davis (1964), Beaumont (1965); Mustelidae, Savage (1957), Schmidt-Kittler (1981); Procyonidae, Baskin (1982), Wozencraft and Decker (1991).

#### METHODS AND MATERIALS

Our assessment of relationships among pinnipeds relies upon outgroup comparison. Flynn et al. (1988) reviewed the relationship of pinnipeds to other arctoids, proposing two principal hypotheses: pinnipeds as the sister group of ursids and pinnipeds as part of a polytomy with other arctoid families. Berta (1991) used the Ursidae and the Amphicyonidae as the first and second outgroups to pinnipedimorphs on the basis of their retaining the excavated basioccipital and presumed loop of the internal carotid artery, a synapomorphy (see Hunt and Barnes 1994, this volume). It is worth mentioning that no extant pinnipeds have the internal carotid loop, and the excavated basioccipital, most extreme in *Enaliarctos*, is presumably lost. Fortunately, strong postcranial evidence that *Enaliarctos* is related to pinnipeds supports the presumed loss of this feature at the level of the Pinnipedia. Proponents of both di- and

monophyly must accept this loss. Thus this feature can in no way be judged to favor a monophyletic Otarioidea. Four synapomorphies link ursids and pinnipedimorphs: (1) shelflike anteromedially placed P<sup>1</sup> protocone, (2) narrow M<sup>1</sup> with longitudinally elongated protocone (Flynn et al. 1988), (3) knoblike acromion process of scapula, and (4) robust olecranon process on ulna (Berta 1991). Wyss and Flynn (1993) used similar evidence to support a sister-group relationship between the Ursoida (defined as the common ancestor of ursids and amphicyonids plus all of its descendants) and the Pinnipedia.

In addition to living representatives of the three pinniped families, we include, as terminal taxa, their extinct relatives and indicate their degree of completeness (Table 1). With two exceptions the monophyly of these taxa is generally accepted. On the basis of comparative anatomical evidence Wyss (1988) questioned the monophyly of "*Monachus*" (indicated by quotes). Berta (1991) recognized *Enaliarctos* as a metataxon [term formulated by Gauthier (1986); see also Gauthier et al. (1988) and Donoghue (1985)] since there is no unambiguous evidence supporting either its monophyly or paraphyly. Initially we included all fossil taxa and in later runs of the data selectively removed them to determine their effect on the tree.

#### PAUP ANALYSIS

We scored 143 skeletal character transformations on a taxon-character matrix (Table 2). Of these characters, 73 were craniodental (64 binary and 11 multistate), 52 were postcranial (48 binary and 4 multistate), and 15 were soft anatomical. Some 160 character transformations were possible.

We subjected the data to Swofford's (1991) computer algorithm PAUP, version 3.0s, using the heuristic search option. In all runs multistate characters were entered as unordered. In the initial PAUP run eight characters, 8, 13, 37, 47, 63, 74, 82, and 138, were excluded since they could not be unambiguously polarized. Our initial PAUP analysis considering all fossil taxa resulted in over 100 most parsimonious trees. Principal differences among the 100 trees were in the position of poorly known odobenids including *Alachtherium*, *Dusignathus*, *Pliopedia*, and *Pontolis*. Later analyses excluded these taxa, including only those at least 53% complete.

TABLE 1. Completeness of fossil taxa studied as a percentage of the number of characters scored (Appendix 1).

Taxon	Percentage Complete	
	Cranial	Postcranial
<i>Enaliarctos</i>	93	78
<i>Pteronarctos</i>	94	0
<i>Thalassoleon</i>	93	71
<i>Imagotaria</i>	91	60
<i>Avikus</i>	77	33
<i>Desmatophoca</i>	90	0
<i>Allodesmus</i>	86	93
<i>Pinnarctidion</i>	53	0
<i>Piscophoca</i>	77	58
<i>Acrophoca</i>	60	73
<i>Homiphoca</i>	90	45
<i>Gomphotaria</i>	63	45
<i>Alachtherium</i>	16	0
<i>Pontolis</i>	23	0
<i>Pliopedia</i>	0	24
<i>Prorosmarus</i>	4	0
<i>Dusignathus</i>	26	0

We obtained the same result, 100+ most parsimonious trees. Each cladogram had a branch length (BL) of 239, a consistency index (CI) of 0.640, and a rescaled consistency (RC) index of 0.554. The RC excludes autapomorphies from the analysis as well as totally homoplastic characters (see Wiley, et al. 1991). A strict-consensus tree is presented in Fig. 2.

#### DISCUSSION

Pinniped monophyly is supported by diverse anatomical data. We discuss below the major groupings shown in Fig. 2. The various characters are numbered as in Appendix 1. Diagnostic characters for the nodes and terminal taxa in Fig. 2 are listed in Appendix 2.

##### Pinnipedimorpha

Berta et al. (1989) proposed the name Pinnipedimorpha as a term for the monophyletic group including *Enaliarctos* and the Pinnipediformes. Postcranial (Berta and Ray 1990) and cranial features (Berta 1991) have been used to diagnose the group (Table 2, Figs. 3–5). We recognize 18 unequivocal characters and 6 equivocal characters diagnosing the Pinnipedimorpha. Among unequivocal synapomorphies are 10 craniodental features: (11) infraorbital foramen large (Fig. 3), (15) anterior palatine foramina anterior of maxillary-palatine suture, (25) round window large with round window fossula developed, (27) basal whorl of scala tympani enlarged, (40) postglenoid foramen vestigial or absent, (43) jugular foramen enlarged, (48) processus gracilis and anterior lamina of malleus reduced, (66) M<sup>1-2</sup> reduced in size relative to premolars, (67) M<sup>1-2</sup> cingulum reduced or absent, and (72) M<sub>1</sub> metaconid reduced or absent.

Unequivocal postcranial synapomorphies of pinnipedimorphs include structural details of the flippers such as (87) greater and lesser humeral tuberosities enlarged (Fig. 4), (88) deltopectoral crest strongly developed (Fig. 4), (90) humerus short and robust, (92) olecranon fossa shallow, (98) digit I on the manus emphasized (Fig. 4), (105) digits I and V on the pes emphasized (Fig. 5), (110) ilium short, and (118) and femoral condyles strongly inclined medially.

An additional 16 equivocal synapomorphies might be diagnostic of this clade but are subject to equally parsimonious alternative distributions. Seven of these characters, not preserved in *Enaliarctos*, we assigned to the less inclusive level of the Pinnipedia: (31) cochlear aqueduct large, (49) middle ear cavity and external auditory meatus with distensible cavernous tissue, (54) deciduous teeth fewer, (60) number of lower incisors reduced, (101) metacarpal I longer than metacarpal II, (103) foreflipper claws short, and (104) manus, digit V, intermediate phalanx strongly reduced.

The oldest known pinnipedimorph, *Enaliarctos*, described on the basis of crania and isolated teeth (Mitchell and Tedford 1977; Barnes 1979), is now known from a nearly complete skeleton collected from the late Oligocene or early Miocene Pyramid Hill Sandstone Member of the Jewett Sand in central California (Berta et al. 1989; Berta and Ray 1990). Other crania and associated lower jaws and postcranial elements referred to this taxon are described from deposits of similar age in coastal Oregon (Berta 1991).

##### Pinnipediformes

The name Pinnipediformes encompasses the ancestor of *Pteronarctos* and all its other descendants, the Pinnipedia. This group can be diagnosed on the basis of 14 characters, two of which are unequivocal: (14) embrasure pit on palate between P<sup>1</sup> and M<sup>1</sup> shallow to absent and (24) mastoid process close to paracipital process, the two connected by a high continuous ridge (state I of multistate character).







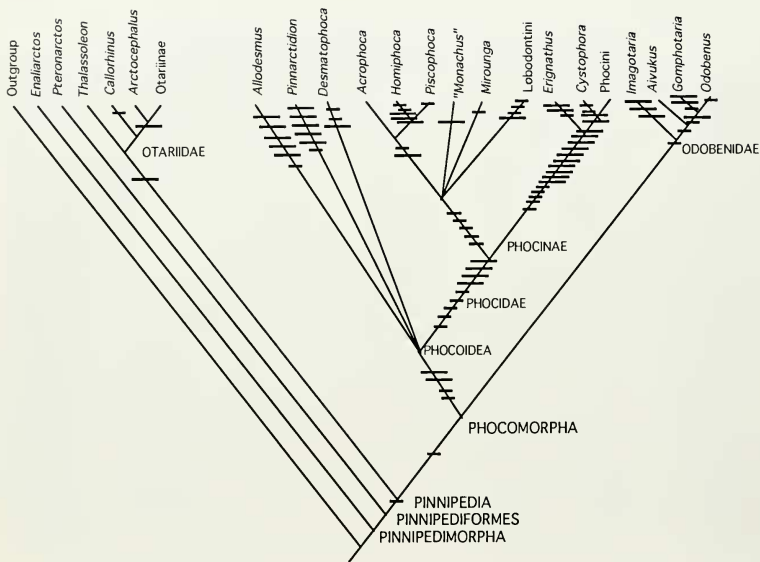


Figure 2. Strict-consensus cladogram of 100 equally parsimonious trees identified by PAUP analysis. Character distributions are listed in Table 2. Short bars, convergences; long bars, reversals.

An additional 12 characters are identified as equivocal synapomorphies at this node. Because 6 of these are unknown in *Pteronarctos* we considered them diagnostic of the Pinnipedia, the least inclusive level at which their distribution can be confirmed (see below).

*Pteronarctos*, the oldest known member of the Pinnipediformes, has been described on the basis of crania and lower jaws (Barnes 1989; Berta, in press) from the Miocene Astoria Formation of coastal Oregon. This taxon provides the first definitive evidence of development of the pinnipeds' unique orbital wall, to which the maxilla contributes significantly (9), and a lacrimal that fuses early in ontogeny and does not contact the jugal (10). Both of these features may be present in *Enaliarctos*, but available material is not sufficiently well preserved to determine this.

#### Pinnipedia

Illiger (1811) proposed the name Pinnipedia to unite the otariids, odobenids, and phocids. Of the nine characters diagnosing this group only three craniodental ones are unequivocal synapomorphies: (30) pit for tensor tympani absent, (59) P<sup>1</sup> lingual cingulum absent, and (71) M<sub>1-2</sub> trigonid suppressed. Potential synapomorphies with other equally parsimonious explanations are (7) fossa nasolabialis absent, (8) fossa muscularis absent,

(16) antorbital processes large and well developed, (63) P<sup>4</sup> protocone shelf absent, (64) P<sup>4</sup> double or single rooted, and (73) M<sub>3</sub> absent.

These characters' being relatively few should not be interpreted as weakness of the case for pinniped monophyly. If only living forms were considered all pinnipedimorph and pinnipediformes synapomorphies described above would represent pinniped synapomorphies. For example, the following synapomorphies, equivocal at the level of the Pinnipedimorpha or Pinnipediformes, are unambiguous at the level of the Pinnipedia: (81) lumbar vertebrae five, (94) olecranon process laterally flattened with expanded distal half, (95) radius with marked anteroposterior flattening and expanded distal half, (109) pubic symphysis unfused, (115) fovea for teres femoris ligament strongly reduced or absent, and (117) greater femoral trochanter large and flattened. These are in addition to the two confirmed pinnipediform synapomorphies and the 18 pinnipedimorph synapomorphies listed in Appendix 1.

#### Otariidae

Relationships among the fur seals and sea lions based on cladistic analysis (Berta and Deméré 1986) are being reanalyzed by Berta using two different, more appropriate outgroups, *Pteronarctos* and the Phocomorpha. Our analysis here supports the latter study in



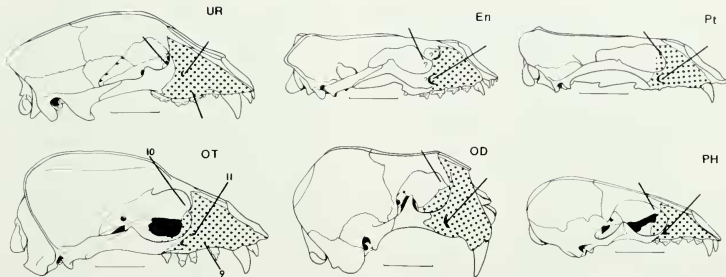


Figure 3. Lateral views of the skulls of representative pinnipeds and a generalized terrestrial arctoid. Extent of maxilla indicated by stippling. En, *Enaliarctos emlongi*; OD, Odobenidae (*Odobenus rosmarus*); OT, Otariidae (*Zalophus californianus*); PH, Phocidae (*Monachus schauinslandi*); Pt, *Pteronarctos goedertae*; UR, Ursidae (*Ursus americanus*). Pinnipedimorph synapomorphies: 10, lacrimal greatly reduced; 11, infraorbital foramen large.

progress in recognizing a sister-group relationship between the southern fur seals, *Arctocephalus* and the sea lions, the Otariinae. The northern fur seal, *Callorhinus*, and the extinct taxon *Thalasseoleon* are positioned as sequential sister taxa to this clade. Two unequivocal osteological characters diagnose the otariid clade: (17) supraorbital processes large and shelllike, particularly among adult males (state 3 of multistate character), and (86) secondary spine on scapula present. Two additional unequivocal synapomorphies based on soft-anatomical characters diagnose the extant Otariidae: (135) pelage units uniformly spaced and (143) trachea with bifurcation of bronchi posterior. An additional character possibly diagnostic of this group is (4) frontals extending anteriorly between the nasals, but this feature is also incidentally developed in some species of *Pteronarctos* (Barnes 1989; Berta, in press).

Basal members of this clade (e.g., *Pithanotaria* and *Thalasseoleon*) are known from the late Miocene in California and Baja California (Repenning and Tedford 1977).

#### Phocomorpha

We propose the name Phocomorpha for the monophyletic group that includes the most recent common ancestor of the odobenids and phocoids plus all its descendants (see Fig. 2). A sister-group alliance between the odobenids and phocoids was originally proposed by Wyss (1987) and endorsed by Flynn et al. (1988) and Berta et al. (1989). Our analysis provides additional characters supporting this hypothesis. We identified nine unequivocal synapomorphies: (26) canals for facial and vestibulocochlear nerves incipiently or completely separated (state 1 of multistate character), (32) canal for cochlear aqueduct merged or nearly merged with round window, (34) petrosal visible in posterior lacerate foramen, (42) basioccipital short, broad, and widened posteriorly, (46) auditory ossicles enlarged, (51) angular process on mandible reduced and elevated above the base of ascending ramus, (124) calcaneal tuber short, (126) caudally directed process of astragalus at least incipiently present (state 1 of multistate character), and (127) baculum enlarged. An additional seven soft-anatomical and behavioral synapomorphies diagnose extant members of this clade: (128) testes abdominal, (129) copulation aquatic, (132) primary hair nonmedullated, (136) subcutaneous fat thick, (139) external pinnae absent, (140) opening of sweat duct proximal, and (141) venous system with inflated hepatic sinus, well-developed caval sphincter,

large intervertebral sphincter, duplicate vena cava, and gluteal route for hindlimbs.

In addition, nine equivocal synapomorphies were identified at this level. Six of these potential osteological synapomorphies require reversals within some phocoids or independent evolution in odobenids and phocids: (76) cervical vertebrae with small transverse processes and neural spines, (77) cervical vertebrae smaller than thoracic or lumbar vertebrae with spinal canal nearly as large as centrum, (79) neural spines on thoracic vertebrae low, (107) hindflipper claws reduced, (114) ischial spine large, and (116) lesser femoral trochanter reduced or absent.

#### Odobenidae

Relationships among walrus are the subject of current study (see Deméré 1994, this volume). Although our data do not resolve relationships at the generic level, we identified six characters as supporting monophyly of the group. Two of these are unequivocal synapomorphies of the postcranial skeleton: (99) pit or rugosity on metacarpal 1 and (125) medial process on calcaneal tuber. An additional three equivocal synapomorphies may diagnose this clade but are subject to other equally parsimonious interpretations. These are (17) supraorbital processes completely absent (state 2 of multistate character), (58) 1<sup>st</sup> terete and caniniform, and (93) diameter of humeral trochlea larger than that of distal capitulum.

Odobenids are first recognized from the middle Miocene of California. Not included in our study and undoubtedly representing a significant position in odobenid evolution is *Neotherium mirum*, new material of which is being studied by L. G. Barnes.

#### Phocoidea

As defined by Wyss and Flynn (1993), the Phocoidea are a clade including the common ancestor of phocids and desmatophocids plus all of its descendants. Seven unequivocal synapomorphies diagnose this clade: (5) posterior termination of nasals posterior to frontal-maxillary contact, (22) pterygoid process with flat, concave lateral margin, (24) mastoid process distant from paroccipital process (state 2 of multistate character), (26) internal auditory meatus absent and canals for vestibulocochlear nerve completely separated (state 2 of multistate character), (35) auditory bulla undelimited basioccipital, (52) bony flange below ascending ramus, and (142) peri-

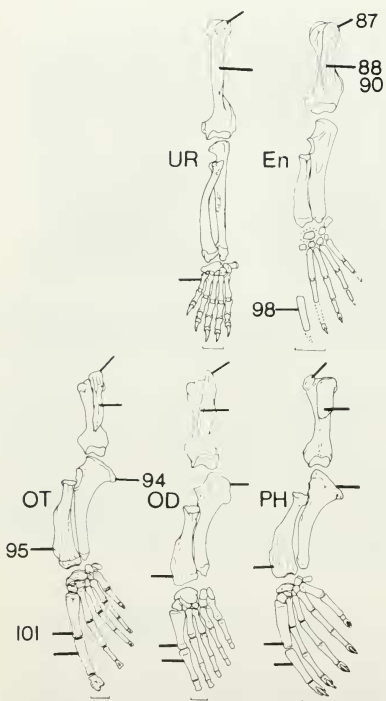


Figure 4. Left forelimb of representative pinnipeds and a generalized terrestrial arctoid in dorsal view. En, *Enaliarctos emlongi*; OD, Odobeninae (*Odobenus rosmarus*); OT, Otariidae (*Zalophus californianus*); PH, Phocidae (*Monachus schauinslandi*); UR, Ursidae (*Ursus americanus*). Pinnipediform synapomorphies: 87, greater and lesser humeral tuberosities enlarged; 88, deltopectoral crest strongly developed; 90, humerus short and robust; 94, olecranon process laterally flattened and posteriorly expanded; 95, distal half of radius expanded; 101, digit I of manus enlarged (see Appendix 1).

cardial plexus well developed. Two of 13 equivocal synapomorphies most likely represent reversals near the base of the clade: (3) nasal processes prominent and (16) antorbital process of frontal large and well developed.

#### Phocidae

Relationships among extant phocids have recently been analyzed cladistically (Muizon 1982a; Wyss 1988b). We identify as a monophyletic clade the archaic seals *Piscophoca*, *Homiphoca*, and *Acrophoca* and hypothesize a sister-group relationship between

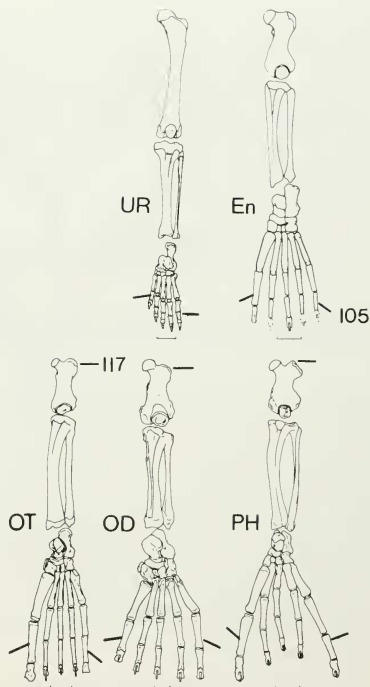


Figure 5. Left hindlimb of representative pinnipeds and generalized terrestrial arctoids in dorsal view. En, *Enaliarctos emlongi*; OD, Odobeninae (*Odobenus rosmarus*); OT, Otariidae (*Zalophus californianus*); PH, Phocidae (*Monachus schauinslandi*); UR, Ursidae (*Ursus americanus*). Pinnipediform synapomorphy: 105, digits I and V of pes elongated (see Appendix 1).

*Piscophoca* and *Homiphoca*. Elephant and monk seals (*Mirounga* and *Monachus*) and extant lobodontines are more closely related to the archaic seal clade than they are to phocine seals. The Phocinae (consisting of *Erignathus*, *Cystophora*, and the Phocini) are recognized as a monophyletic group in agreement with Burns and Fay (1970), Muizon (1982a), and Wyss (1988b). The Phocidae are diagnosed by 26 derived characters, eight of which are unequivocal synapomorphies for the group: (20) alisphenoid canal absent, (23) mastoid heavily pachyostotic, (28) basilar cochlear whorl directed transversely, (29) dorsal region of petrosal expanded, (33) opening of cochlear fenestra outside tympanic cavity, forming a cochlear foramen, (41) pit for tympanohyal anterior to stylomastoid foramen, (112) insertion for ilial psoas muscle on ilium, and (126)

process of astragalus directed caudally (state 2 of multistate character). Eleven other characters are potential synapomorphies.

This phylogeny implies many character reversals at the base of the phocine seal clade, a pattern discussed further below.

Our apparent endorsement of "monachine" monophyly is based on our not treating "*Monachus schauinslandi*" as a separate taxon. Outside the subfamily Phocinae, we don't attribute much significance to the intraphocid relationships depicted in Figure 2. For example, our results reveal a puzzling arrangement in which reported fossil lobodontines (*Homiphoca*, *Acrophoca*, and *Piscophoca*) are not nested among extant lobodontines. Of the three synapomorphies linking fossil lobodontines, none is unequivocal. One character, (53) mandibular condyle elevated above tooth row, requires a reversal among modern lobodontines. For another character, (64) P<sup>4</sup> double rooted, fossil lobodontines represent an intermediate transformation, P<sup>4</sup> becoming single rooted among modern lobodontines and other phocids. A third character, (36) mastoid lip covering or partially covering external cochlear foramen, either reverses in "*Monachus*" and *Mirounga* or originated independently among fossil and modern lobodontines. Thus, this arrangement separating fossil from extant lobodontines is poorly supported.

Although phocids have a temporal range extending back into the middle Miocene, much of the material is fragmentary. Later archaic phocids are represented by abundant well-preserved material of *Acrophoca* and *Piscophoca* from the early Pliocene of Peru (Muizon 1981) and of *Homiphoca* from late Miocene or early Pliocene of South Africa (Hendey and Repenning 1972; Muizon and Hendey 1980).

#### EXPERIMENTAL MANIPULATIONS OF DATA

We performed several experimental manipulations of the data set. In one run we forced otarioid monophyly. The strict-consensus tree that resulted from 100 trees was 34 steps longer than our preferred tree. In another run to address the question of diphyly we forced the monophyly of musteloids and phocids. The strict-consensus tree that resulted from 100 trees was 77 steps longer than our preferred tree. Finally, in an attempt to determine the role of fossils in pinniped phylogeny, we excluded all fossil taxa. The resulting tree showed no major change in topology.

#### ASSESSING THE PATTERN OF HOMOPLASY

There has been a widespread recent tendency among carnivorous systematists to assume pervasive convergence of pinnipeds (Wyss 1989), sometimes when such assumptions are unnecessary. Wozencraft (1989:504) saw the controversy of pinniped monophyly vs. diphyly as centering "on the treatment of parallel and convergent characters," suggesting that monophyly is favored only if aquatic adaptations are not excluded. In our view this line of reasoning is flawed in two respects: (1) it assumes convergence at the outset, something for which one needs a phylogeny to uncover, and (2) it assumes that because a particular structure has some "adaptation" or functional significance it probably originated independently and is therefore irrelevant phylogenetically. The implausibility of the latter view is patent: taken to its logical extreme one would have difficulty in defending the monophyly of even noncontroversial groups of pinnipeds. The posterior process on the phocid calcaneum, for example, has important functional implications in keeping the hindlimb posteriorly extended, yet it has never been rejected as supporting a common origin for the group. We regard the distinctively reduced fifth intermediate phalanx on the pinniped manus (among numerous other features) as equally deserving of serious phylogenetic consideration.

Barnes (1989: fig. 9) assumed convergence even when such an

assumptions was unnecessary. For example, he viewed enlarged ear ossicles as originating independently in the Desmatophocinae, walrus (though he showed these taxa as sister groups), and in a clade including the Alloedeminae and *Pinnarctidion*, though no characters bar a linkage between this clade and his desmatophocine-walrus clade. Thus three originations of this character are proposed where one would have sufficed. Additionally, the assumption of convergence implies that the ossicles enlarged independently in the phocids, too. Thus assuming convergence may violate parsimony. There is nothing to prevent one from suggesting that any character has originated independently in every terminal taxon.

We mapped patterns of homoplasy on our strict-consensus tree (Fig. 2). Reversals exceed convergences 48 to 41. Our analysis establishes that the majority of reversals, excluding those confined to terminal taxa, occurred among the phocine seals, a pattern previously noted by Wyss (1988b) and referred to by Howell (1929) as "retrogressive" evolution. Reversals are more than twice as common here as at any other place on the tree. Nearly all of these reversals occurred at the base of the phocine clade rather than among terminal taxa. These reversals are confined largely to details of flipper structure (see Wyss 1994, this volume, for further discussion) and include (85) supraspinous fossa slightly larger than infraspinous fossa, (89) supinator ridge of humerus well developed, (91) entepicondylar foramen present, (100) metacarpal heads keeled with trochleated phalangeal articulations, (101) metacarpal I equal in length to others, (103) foreflipper claws long, (104) intermediate phalanx of digit V unreduced, (107) hindflipper claws unreduced, and (108) pes with short, rounded metatarsal shafts with rounded heads, associated with trochleated phalangeal articulations.

#### MOLECULAR DATA

Studies of DNA hybridization, amino acid sequences, and chromosomes support pinniped monophyly [see Wyss (1987) for a more detailed review], although there is disagreement as to which group of terrestrial arctoids pinnipeds are most closely related, or, in the case of chromosomal work, to which pinnipeds the walrus is most closely related. Armason and Widgren (1986) demonstrated that pinnipeds share four highly repetitive DNA components unique to pinnipeds or shared with mustelids (with the exception of *Mephitis*). De Jong (1982) found that in the eye-lens protein alpha lens crystallin there are two amino acid replacements uniquely shared by phocids and otariids (the walrus was not sampled). In addition these workers discovered a similarity between the mustelid *Mustela* and the procyonid *Bassariscus* in two amino acid replacements that differ from replacements seen in the other carnivores sampled (de Jong 1986). Significantly, phocids do not share these similarities, thus failing to support a phocid-mustelid alliance. More recently, sequencing by Keith et al. (1991) of the milk protein beta lactoglobulin supports a close relationship between phocids and otariids. Their results indicate that these groups are closer to canids than to ursids. Neither the walrus nor mustelids have yet been sampled (Keith, pers. comm.).

The karyological similarity among pinnipeds supports pinniped monophyly. Fay et al. (1967) supported *Odobenus* as a karyological intermediate between phocids and Otariids. Armason (1974), however, disputed this conclusion, arguing for a stronger similarity between otariids and phocids.

We hope future molecular and karyological data will be analyzed cladistically.

#### CONCLUSIONS

In summary, we believe that the cases for otarioid monophyly and pinniped diphyly have not been established. We urge that those

continuing to defend these hypotheses analyze the data explicitly and include character distributions among appropriate outgroups and all members or potential members of the ingroups. Pinniped monophyly is supported overwhelmingly by diverse anatomical data and is strongly suggested by biochemical data as well.

The historical expectation of convergence among pinnipeds has clouded the interpretation of their relationships. In the context of a well-corroborated phylogenetic hypothesis it seems that the pattern of homoplasy argues for character reversals occurring as commonly as convergences.

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## APPENDIX 1

Craniodental, postcranial, and soft-anatomical characters examined among recent and fossil pinnipeds. The discussion of a character's hypothesized sequence of transformation is an *a posteriori* assessment based on the distribution of that feature on our strict-consensus tree.

### Skull

1. Premaxilla–nasal contact. 0 = extensive, 1 = reduced. In *Odobenus*, *Allodesmus*, and the Phocidae (Wyss 1987:7, 15, fig. 5) the contact between the premaxilla and nasal is short and narrow. Wozencraft (1989) incorrectly identified phocids and lutrines as sharing a reduced premaxilla–nasal contact. Among lutrines, the premaxilla–nasal contact is reduced only in the sea otter, *Enhydra*. Wyss noted that the premaxillae of *Odobenus* differ from those of phocids in being broadly sutured with the nasals inside the nasal cavity; in phocids no such internal contact occurs. An undescribed fossil odobenid of the genus *Imagotaria* (LACM 118675) shows the primitive condition of a broad contact between the premaxilla and nasals. This derived feature we judge diagnostic of *Allodesmus* + *Desmatophoca* + phocids (Phocoidea) and as an autapomorphy of *Odobenus* or a reversal in *Imagotaria*.

2. Premaxilla. 0 = ascending process visible laterally along entire length, 1 = ascending process dips into nasal aperture. According to Muizon (1982a:186, 187, fig. 4), in “monachines” the premaxilla–maxilla suture is, in its medial part, located inside the nasal aperture. This condition applies strictly to neither “*M.*” *monachus* nor *Homiphoca* and according to our most parsimonious tree is likely primitive for phocids. Although most phocines show the primitive condition of this character, variation exists with *Histicphoca* and *Pagophilus* possessing the derived “monachine” condition (Muizon 1982a). *Allodesmus* and *Desmatophoca* show a similar derived condition (see Barnes 1972, fig. 4; 1987, fig. 1). The derived state is a synapomorphy for phocoids with several reversals.

3. Nasal processes of premaxilla. 0 = not prominent, 1 = prominent, protrude dorsal and anterior to alveolar margin, 2 = well elevated anterior and dorsal to alveolar margin. As Howell (1929) first noted, there is a well-defined process formed by the premaxillary tips in *Zalophus* that is absent in *Phoca*. In *Odobenus*, the nasal processes are elevated well above the alveolar incisor margin, owing to the great modifications of the snout. As noted by Repenning and Tedford (1977:18), this condition distinguishes *Odobenus* from other odobenids.

Prominent nasal processes do not occur in ursids, *Enaliarctos*, *Allodesmus*, *Desmatophoca*, or phocids. An intermediate condition in which the nasal process are prominent and protrude (but are not elevated) dorsal and anterior to the incisor alveolar margin distinguishes *Pteronarctos*, otariids, odobenids, and phocids primitively (i.e., *Imagotaria*, *Aivukus*, and *Homiphoca*). Hence the presence of prominent nasal processes is most parsimoniously interpreted as having originated at the level of Pinnipediformes and having been lost among phocids. Its presence in *Homiphoca* is regarded as an independent derivation.

4. Frontals. 0 = do not extend anteriorly between nasals, 1 = extend anteriorly between nasals. Otariids display a characteristic W-shaped nasofrontal contact, in which the frontals extend anteriorly between the nasals (King 1983:151, fig. 6.4). In other pinnipeds and most terrestrial carnivorans the frontals and nasals do not show this relationship. Wozencraft (1989:521) incorrectly maintained that odobenids and otariids share the derived condition, a W or divergent shape. Both juveniles and adults of *Odobenus*, as well as *Imagotaria*, maintain a horizontal line of contact between the nasals and the frontals.

The derived condition is an autapomorphy for all taxa more closely related to living otariids than to other pinnipeds. However, it should be noted that in at least one nonotariid, *Pteronarctos goeertae* (see Barnes 1989: figs. 1, 2), the frontals extend slightly between the nasals, which might be interpreted as incipient development of the derived condition; accordingly, we scored the condition scored in this taxon as variable.

5. Posterior termination of nasals. 0 = at or near frontal–maxillary contact, 1 = posterior to frontal–maxillary contact. The nasals' narrowing greatly posteriorly and terminating far posterior of the frontal–maxillary contact is a synapomorphy uniting *Desmatophoca*, *Allodesmus*, and phocids (Berta 1991). In terrestrial carnivorans, *Enaliarctos*, *Pteronarctos*, otariids, and odobenids the nasals terminate at or near the broad frontal–maxillary contact.

6. Palatine process of maxilla. 0 = terminates at last molar, 1 = extends behind last molar. 2 = developed as a shelf (pterygoid process of maxilla, Barnes 1987). Barnes (1979:23) noted that in *Pinnarctidion bishopi* a “wide, thin, squared posterolaterally projecting shelf of the palate is beneath each orbit.” Barnes (1987) described this structure, better developed in *Desmatophoca brachycephala*, as an expansive pterygoid process of the maxilla that forms a thin infraorbital shelf with a prominent posterolateral corner. He observed that this structure is more prominent in *D. brachycephala* than in *Allodesmus packardii* and *D. oregonensis*.

Pinnipediformers are distinguished ancestrally from terrestrial carnivorans by having an intermediate condition (1) in which the palatine process of the maxilla extends posterior to the last molar. Berta (1991) recognized the presence of a palatine shelf in *Pinnarctidion*, *Desmatophoca*, *Allodesmus* as a second derived condition (2).

7. Nasolabialis fossa. 0 = present, 1 = absent. The nasolabialis fossa, described in *Enaliarctos* by Mitchell and Tedford (1973:220, 234) as a “rather deep fossa for the quadratus labii superioris muscle,” is “located on the rostrum, just anterior to the antorbital rim.” Among terrestrial carnivorans the nasolabialis fossa is present in the archaic ursids *Allocoyon* and *Cephalogale*. It is present in *Enaliarctos*, *Pteronarctos*, and *Pinnarctidion* and absent in all other pinnipediformers (Berta 1991), a distribution suggesting that absence of the nasolabialis fossa is a pinniped synapomorphy. We consider its presence in *Pinnarctidion* a reversal to the primitive condition.

8. Fossa muscularis. 0 = present, 1 = absent. In ursids, “immediately behind the lacrimal fossa is a shallow pit, the fossa muscularis, in which the inferior oblique muscle of the eye arises; the thin dry floor of this pit is usually broken through on dry skulls, and then resembles a foramen. . . . In *Ursus* it is relatively enormous, as large as the lacrimal fossa” (Davis 1964:49). The fossil ursid *Cephalogale* has behind its lacrimal fossa a slight depression delimited by a ventrally floored ridge, possibly the precursor of the deep, posteriorly positioned fossa muscularis seen in *Enaliarctos* and *Pteronarctos*.

Because this character could not be unambiguously polarized from our outgroups we excluded it from the initial run of characters.

9. Maxilla. 0 = does not contribute significantly to medial orbital wall, 1 = contributes significantly to orbital wall and forms anterior orbital rim. In terrestrial carnivorans the maxilla is usually limited in its posterior extent by contact of the jugal or palatine with the lacrimal (Wyss 1987). Sutures in the orbital region of available specimens of *Enaliarctos* are fused, hence the arrangement of bones in this region cannot be determined. An undescribed species of *Pteronarctos* (USNM 335432) shows sutures in this region; although a lacrimal is clearly present it contacts neither the palatine nor the jugal.

Therefore, we identify the derived condition as a synapomorphy of *Pteronarctos* plus the pinnipeds (= Pinnipediformes). Additional specimens of *Enaliarctos* may demonstrate this to be a pinnipediform synapomorphy. Barnes (1989) used this feature as an "otarioid" synapomorphy.

10. Lacrimal. 0 = distinct, contacts jugal, 1 = fuses early in ontogeny to maxilla and frontal, greatly reduced or absent; does not contact jugal. Associated with the pinniped configuration of the maxilla is the great reduction or absence of the lacrimal. King (1971) demonstrated the presence of a lacrimal in all extant otariids, showing that in them, unlike terrestrial carnivorans, the lacrimal tends to fuse relatively early in ontogeny to the maxilla and frontal, obscuring it. In no otariid, however, does it contact the jugal or palatine. As observed by Wyss (1987), a lacrimal is difficult to identify in phocids and odobenids. Wozencraft (1989:522) argued that the lacrimal, including in otariids and odobenids an orbital flange, is present in these groups. As noted above, however, this condition is fundamentally different from that in terrestrial carnivorans. In his discussion of a related character, Wozencraft incorrectly argued that lack of contact between the jugal and lacrimal also characterizes ursids and mustelids. On the contrary, terrestrial carnivorans can be distinguished from pinnipeds by their lacrimal's contacting the jugal or being separated from it by at most a thin sliver of the maxilla. The distinctiveness of the orbital mosaic in "otarioids" was highlighted even by a proponent of otarioid monophyly (Barnes 1989); it occurs, however, in phocids also.

Presence of a lacrimal in *Enaliarctos* cannot be determined. In *Pteronarctos repenningi* (USNM 335432) the lacrimal is distinct but fails to contact the palatine or the jugal. The derived condition is a synapomorphy linking *Pteronarctos* and pinnipeds (Berta 1991).

11. Infraorbital foramen. 0 = small, 1 = large. A large infraorbital foramen is a pinnipediform synapomorphy (Berta 1991). Infraorbital foramina are small in most terrestrial carnivorans except amphicyonodont ursids (see Tedford et al., 1994, this volume).

12. Orbital vacuities. 0 = absent, 1 = present. Wyss (1987:16, fig. 5) noted in pinnipeds an unossified space (orbital vacuity) in the ventral orbital wall near the juncture of the frontal, maxilla, and palatine. Such orbital vacuities characterize pinnipediforms exclusive of *Enaliarctos*, *Pteronarctos*, *Imagotaria*, *Aivukus*, and *Desmatophoca* (Berta 1991).

Wozencraft (1989:522) distinguished differences among pinnipeds in the formation of orbital vacuities. According to him, an enlarged sphenopalatine foramen eclipses the orbitosphenoid (creating an orbital vacuity) in otariids and odobenids but not phocids. Phocids do, however, possess an orbital vacuity that variably includes the sphenopalatine foramen.

The distribution of this character suggests that orbital vacuities evolved independently in the three major pinniped groups, among otariids, in *Odobenus*, and among some phocoids (*Allodesmus* + phocids).

13. Palate. 0 = parallel-sided, 1 = posteriorly widening. In phocids, *Allodesmus*, and to a lesser degree *Pinnarctidion*, unlike otariids and odobenids, the palate widens posteriorly, a derived

condition (Wyss 1987). In contrast, Wozencraft (1989:521) identified a posteriorly broad palate as the primitive condition among carnivorans. While we recognize that the palate diverges widely in most terrestrial carnivorans, it does not in ursids or amphicyonids. *Enaliarctos* and otariids retain what we interpret to be the ancestral condition for the Pinnipedimorpha. This condition is a synapomorphy uniting phocoids. Because of the variability among out-groups we polarized this character on a second run of characters.

14. Embrasure pit between  $P^1$  and  $M^1$ . 0 = deep, 1 = shallow or absent. *Enaliarctos* is distinguished from *Pinnarctidion*, *Pteronarctos* (Barnes 1979, 1989) and all other pinnipediforms by its deep embrasure pit for the crown of  $M^1$  between  $P^1$  and  $M^1$ . Barnes further noted that reduction of this pit indicates a corresponding reduction in the size of the lower carnassial. Terrestrial carnivorans typically possess a deep embrasure pit on the palate. We here regard this character as a *Pteronarctos* + pinniped synapomorphy.

15. Anterior palatine foramina. 0 = on or slightly posterior to maxillary-palatine suture, 1 = anterior of maxillary-palatine suture. The major palatine foramen (= anterior palatine foramen or anterior opening of the palatine canal; see Novacek 1986) is situated anterior of the maxillary-palatine suture in otariids, phocids, and odobenids but lies on the suture in other arctoids (Davis 1964; Burns and Fay 1970). Wozencraft (1989) incorrectly argued that the primitive condition is characteristic of all three extant pinniped families.

Although Barnes (1979) distinguished *Enaliarctos mitchelli* from *E. meadi* by its paired posterior palatine foramina (= anterior palatine foramina), additional material of the latter shows the derived condition to characterize all pinnipediforms (Berta 1991).

16. Antorbital process of the frontal. 0 = absent or small, 1 = large and well developed. Barnes (1979) noted that the antorbital process (often referred to as the lacrimal process) of *Pinnarctidion* is not as broadly based as in *Enaliarctos* and that it protrudes further from the side of the skull. We maintain that well-developed antorbital processes do not occur in *Enaliarctos* or *Pinnarctidion*. As coded here the derived condition occurs in otariids and odobenids. We interpret it as a convergence of those two families or as having been present in the Pinnipedia primitively then reversed in the Phocidea. Although the antorbital process is lacking in "*Monachus*" it occurs among some phocids (*Erignathus*, *Mirounga*, *Lobodontini*), we infer as a secondary derivation.

17. Supraorbital process. 0 = distinct and blunt, 1 = reduced to a supraorbital ridge, 2 = completely absent, 3 = large and shelllike. The primitive condition seen in terrestrial carnivorans is a frontal with a small, rounded supraorbital process. State 1 in which the supraorbital process is reduced is seen in *Enaliarctos*, *Pteronarctos*, *Allodesmus*, *Desmatophoca*, and *Pinnarctidion*. Phocids and odobenids except *Gomphotaria* have lost the process completely (2). The large shelllike supraorbital processes (3) of otariids we consider an autapomorphy of the group.

Barnes (1989:18) argued that absence of supraorbital processes is primitive for otarioids. He noted that *Pteronarctos* can be distinguished from *Enaliarctos* on the basis of its larger supraorbital processes. Additional specimens of these taxa (Emlong collection), however, show that this distinction does not hold. *Enaliarctos* and *Pteronarctos* both possess small tuberosities or ridges in this region. Therefore we interpret the reduction of supraorbital ridges in *Enaliarctos*, *Pteronarctos*, and archaic phocids as independently derived. Alternatively, the condition in *Enaliarctos* and *Pteronarctos* may be primitive for pinnipediforms.

18. Least interorbital width. 0 = occurs in posteriormost portion of interorbital septum, 1 = occurs in the anterior half of the

interorbital septum. Burns and Fay (1970) noted that in *Cystophora* and the Phocini, the interorbital distance is least in the anterior half of the interorbital septum. In other pinnipedimorphs and in other carnivores the interorbital region is narrowest in the posteriormost section.

19. Foramen rotundum. 0 = separate from anterior lacerate foramen, 1 = merged with anterior lacerate foramen [see also discussion of Barnes' character (d) under Otarioid Monophyly].

*Pinnarctidion* can be distinguished from *Enaliarctos* and other pinnipeds by its having the foramen rotundum separate from the anterior lacerate foramen. Canids and ursids also share the condition of a separate foramen rotundum (Barnes 1979, 1987).

Our phylogeny implies that *Pinnarctidion* is an exception among pinnipedimorphs in displaying the primitive condition. We suggest that the derived condition is a pinnipedimorph synapomorphy, reversed in *Pinnarctidion*.

20. Alisphenoid canal. 0 = present, 1 = absent. Since the alisphenoid canal is widespread among terrestrial carnivores, including all ursoids, its presence in pinnipeds is undeniably primitive. Thus presence of an alisphenoid canal in the "Otarioidea" does not support the unity of this group, as argued by Barnes (1989). Absence of the alisphenoid canal among phocids has long been regarded as a synapomorphy of that group or as a synapomorphy of mustelids + phocids.

21. Mastoid visible in dorsal view of skull. 0 = no, 1 = yes. A lateral swelling of the mastoid is visible in a dorsal view of the skull in phocine but not "monachine" phocids (King 1966; Burns and Fay 1970). This is regarded as the derived condition because it does not occur in terrestrial carnivores or other pinnipedimorphs.

22. Pterygoid process. 0 = rounded with convex lateral margin, 1 = flat with concave lateral margin. According to Barnes (1989) *Pinnarctidion*, *Allodesmus*, and *Desmatophoca* are distinguished from other "otarioid" pinnipeds by their flat pterygoid strut with a concave lateral margin. We found that phocids also possess the derived condition.

23. Mastoid. 0 = composed of cancellous bone, 1 = heavily pachyostic. A pachyostotic mastoid is unique to phocids (Burns and Fay 1970).

24. Mastoid process. 0 = close to paroccipital process, the two connected by a low discontinuous ridge, 1 = close to paroccipital process, the two connected by a high continuous ridge, 2 = distant from paroccipital process. In ursids and other artoids the mastoid process fails to form a complete ventral ridge that extends back to the paroccipital process as it does in otariids and odobenids. A high, continuous ridge joins these processes in *Pteronarctos*, otariids, and odobenids and is thus likely primitive for pinnipedimorphs. In *Pinnarctidion* the two processes are separated and not broadly continuous, although they are connected by a crest (Barnes 1979).

The plesiomorphic condition occurs in terrestrial carnivores, including ursids (Mitchell and Tedford 1973:248) and *Enaliarctos*. State 1 occurs in *Pteronarctos*, otariids, and odobenids. State 2 occurs in phocids, *Pinnarctidion*, *Allodesmus*, and *Desmatophoca*.

25. Round window. 0 = unenlarged, 1 = large, with round window fossula. In pinnipeds the round window is large and the fossula apparently serves to shield the secondary tympanic membrane from the distensible cavernous tissue of the middle ear (Repenning 1972). This fossula is absent in other carnivores except perhaps *Potamothereium* and the lutrines, in which a very shallow fossula may incipiently (and variably) be present (Tedford 1976; pers. obs.). In these latter forms the round window is not greatly enlarged. Among pinnipeds the round window is most expanded in phocids but it is also very large in odobenids. The derived condition is a pinnipedimorph synapomorphy.

26. Internal auditory meatus. 0 = present and canals for vestibulocochlear and facial nerves closely adjacent, 1 = present and canals for vestibulocochlear and facial nerves incipiently separated, 2 = absent and canals for vestibulocochlear and facial nerves completely separated. Derived state 1 occurs in *Odobenus* and *Imagotaria* (Repenning and Tedford 1977); state 2, in phocids, *Allodesmus*, *Desmatophoca*, and *Pinnarctidion*.

27. Basal whorl of scala tympani. 0 = unenlarged, 1 = very enlarged. The basal whorl of the cochlea is greatly enlarged in width and diameter in all pinnipeds (Repenning 1972). This expansion appears to be most marked in odobenids and phocids. Pending comparative measurements, it may actually prove to be a phocid + odobenid synapomorphy.

28. Basal cochlear whorl. 0 = posterolateral to long axis of skull, 1 = transversely directed. In phocids, the basal whorl of the cochlea runs transverse to the long axis of the skull, rather than posterolaterally as in other carnivores including otariids and odobenids (Repenning 1972). The derived condition is thus a phocid synapomorphy.

29. Dorsal region of petrosal. 0 = unexpanded, 1 = expanded. Repenning and Ray (1977) observed that "*Monachus*" *schauinlandi* can be distinguished from all other phocids by its having a relatively unexpanded dorsal petrosal region (see also discussion in Wyss 1988: fig. 2).

30. Pit for tensor tympani. 0 = present, 1 = absent. In terrestrial carnivores the tensor tympani originates from a small pit in the petrosal anterior to the oval window. In pinnipeds this pit is lost and the muscle originates with the bony eustachian tube (Repenning 1972). Among pinnipedimorphs, this pit is present in *Enaliarctos* (Mitchell and Tedford 1973) and *Pteronarctos* (Berta 1991). Hence, the derived condition is a pinniped synapomorphy.

31. Cochlear aqueduct. 0 = small, 1 = large. As noted by Fleischer (1973) the pinnipeds' cochlear aqueduct is greatly enlarged. Pending a quantified survey among the carnivores of cochlear aqueduct dimensions, we tentatively regard this character as a pinniped synapomorphy.

32. Canal for cochlear aqueduct. 0 = separate from round window, 1 = merged or nearly merged with round window. In pinnipeds the cochlear aqueduct is only narrowly separated from the round window, and in phocids at least the canal for the aqueduct strictly speaking does not exist (Fleischer 1973). In terrestrial carnivores the cochlear aqueduct is a very narrow canal that passes about half the width of the promontorium through the petrosal itself. In phocids and *Odobenus* the connection of the cochlear aqueduct to the cochlea is via the round window, although *Odobenus* may still have a narrow, bony separation between the round window and the cochlear aqueduct. Otariids retain a condition more primitive than in other pinnipeds in that their cochlear aqueduct still pierces the petrosal. Accordingly, the derived condition is an odobenid + phocid synapomorphy.

33. External cochlear foramen. 0 = absent, 1 = present. Phocids display a unique external cochlear foramen (Burns and Fay 1970), an opening at the bulla-mastoid junction just posterior to the auricular foramen and stylo-mastoid foramen.

34. Petrosal. 0 = not visible in posterior lacerate foramen, 1 = visible in posterior lacerate foramen. Burns and Fay (1970) and King (1966) have discussed the visibility in phocids of the petrosal in ventral view through the posterior lacerate foramen. The petrosal is also visible in *Odobenus* and its fossil allies (Repenning and Tedford 1977), *Pinnarctidion*, *Desmatophoca*, and *Allodesmus* (Wyss 1988b; Berta 1991). In the primitive condition seen in terrestrial carnivores, *Enaliarctos*, *Pteronarctos*, and otariids the petrosal is not visible in ventral view from the posterior lacerate foramen.



35. Auditory bulla. 0 = abuts basioccipital, 1 = underlaps basioccipital. In ventral view, the bulla abuts the basioccipital in ursids, *Enaliarctos*, *Pteronarctos*, otariids, and odobenids. In the derived condition seen in *Pinnarctoides*, *Desmatophoca*, *Allodesmus*, and phocids, the bulla underlaps the basioccipital (Berta 1991).

36. Mastoid lip. 0 = not extensive, 1 = covers or partially covers external cochlear foramen. As noted by numerous workers (Repenning and Ray 1977; Muizon and Henedy 1980; Muizon 1982a) extant lobodontine phocids uniquely show a mastoid lip overlapping the posterior bullar wall and covering the external cochlear foramen. The derived condition is also seen in fossil lobodontines, *Homiphoca* (Muizon and Henedy 1980), *Acrophoca*, and *Piscophoca* (Muizon 1981). The primitive condition in which the mastoid lip does not cover the external cochlear foramen is seen in *Mirounga*, "*Monachus*," and phocines (Wyss 1988).

37. Caudal entympanic, 0 = uninflated, 1 = inflated, 2 = greatly inflated. *Odobenus*, *Allodesmus*, and *Pinnarctoides* show an intermediate condition, a bulla slightly inflated, whereas in phocids the bulla is greatly inflated (Wyss 1987:24). Wozencraft (1989:523) identified inflation of the caudal entympanic as a feature shared by canids, procyonids, some mustelids, and phocids. We agree that some mustelids and procyonids possess an inflated entympanic (although not necessarily primitively), but in ursids the caudal entympanic is not inflated. From this distribution we interpret the inflation of the entympanic in some mustelids and procyonids as an independent acquisition.

We excluded this character from the initial run of characters because of the variability among mustelid and procyonid outgroups.

38. Posterior opening of carotid canal. 0 = visible in ventral view, posteromedial process present, 1 = not visible in ventral view, posteromedial process absent. In the phocines excluding *Erigonathus* the posterior opening of the internal carotid canal is not visible in ventral view owing to prominent bullar inflation (Burns and Fay 1970). In other pinnipeds a bony shelf projects from the dorsal and/or medial margin of the aperture toward the posterior lacerate foramen. Hence we recognize the derived condition as a synapomorphy of the Phocini plus *Cystophora*.

39. Squamosal-jugal articulation. 0 = splintlike, 1 = mortised, 2 = exaggeratedly mortised. Barnes (1979:23) described in *Enaliarctos* and otariids a splintlike arrangement of squamosal and jugal in which the jugal tapers to a sharp point and the squamosal does not touch the postorbital process of the jugal. In *Pinnarctoides bishopi* the squamosal does not taper but ends in a blunt, vertically expanded tip. It not only touches the postorbital process of the jugal but fits into a shallow notch on its posterior side. Barnes further observed that the mortised articulation in which both the postorbital process of the jugal and the zygomatic process of the squamosal are expanded dorsoventrally is more greatly developed in *Allodesmus* than in phocids.

Condition 1 unites *Pinnarctoides* and *Desmatophoca*; condition 2 unites *Allodesmus* and the phocids (Berta 1991). Barnes (1989:18) argued that a mortised squamosal-jugal articulation occurs in the Odobenidae also, an observation with which we disagree [e.g., *Imagotaria* (Repenning and Tedford 1977: fig. 4)].

40. Postglenoid foramen. 0 = large, 1 = vestigial or absent. The primitive condition occurs in *Cephalogale*, *Allocoyon*, and amphicyonids. In *Enaliarctos* the postglenoid foramen is small (Mitchell and Tedford 1973:249). It is absent in "*Monachus*" but relatively large in *Phoca*, suggesting it may be secondarily derived among some phocids. We have coded the Phocini as polymorphic for this character since this foramen was present in most but not all specimens of *Histicophoca* examined by Burns and Fay (1970). Berta (1991) identified the derived condition as a pinnipedimorph synapomorphy.

41. Pit for tympanohyal [= vagina processus styloidei of Mitchell and Tedford (1973:227, fig. 9) and Mitchell (1968)]. 0 = closely associated with styломastoid foramen, 1 = anterior to styломastoid foramen. In ursids (including *Cephalogale*) the pit for the tympanohyal lies with the styломastoid foramen in a common fossa (Mitchell and Tedford 1973:246), contradicting Wozencraft's (1989) statement that ursids are characterized by the derived condition. In all pinnipedimorphs except phocids the tympanohyal pit lies very close and posteromedial to the styломastoid foramen. By contrast, in phocids the tympanohyal lies ventral and anterior to the styломastoid foramen.

42. Basioccipital. 0 = long and narrow, 1 = short, broad, and widened posteriorly. The derived condition unites odobenids, phocids, *Allodesmus*, and *Desmatophoca* (Wyss 1987; Berta 1991).

43. Jugular (= posterior lacerate) foramen. 0 = unenlarged, 1 = enlarged, 2 = further enlarged medial to basioccipital. Enlargement of the jugular foramen is a pinnipedimorph synapomorphy (Wyss 1987; Berta 1991). We disagree with Wozencraft's (1989:523) claim that a large posterior lacerate foramen also characterizes canids and ursids.

A secondary modification of this feature in which the posterior lacerate foramen extends medial to the tympanic bulla unites the phocines (see Wyss 1988b:16).

Barnes' (1989) use of an expanded posterior lacerate foramen as an "otarioid" synapomorphy substantiates our recognition of the derived condition as distinct from that seen in terrestrial carnivorans and validates its use in phylogenetic analysis. If this feature is reliable enough to diagnose "otarioids," it is equally valid in diagnosing pinnipedimorphs.

44. Basioccipital-basisphenoid region. 0 = strongly concave, 1 = flat to convex. Burns and Fay (1970) noted that in all phocines the basioccipital-basisphenoid region is flat to convex. In ursids, *Enaliarctos*, "monachines," otariids, odobenids, *Allodesmus*, and *Desmatophoca* this region is strongly concave (Davis 1964; Barnes 1972; Repenning and Tedford 1977; Barnes 1987; Wyss 1988b). Hence, the derived condition is a phocine synapomorphy.

45. Paroccipital process. 0 = small, 1 = enlarged posterolaterally. Related to conformation of the mastoid process (character 24) is the morphology of the paroccipital process. In ursids, *Enaliarctos*, *Pteronarctos*, otariids, odobenids, and phocids the paroccipital processes are small. In *Desmatophoca*, *Allodesmus*, and *Pinnarctoides* (Berta 1991) these processes are enlarged posterolaterally.

46. Auditory ossicles. 0 = unenlarged, 1 = enlarged. Enlarged ossicles unite odobenids, *Allodesmus*, phocids, *Desmatophoca*, and *Pinnarctoides*. Related to this character is the size of the epytympanic recess containing the ossicles. Many mustelids, however, have large epytympanic recesses (sinuses) without enlarged ossicles.

47. Muscular process of malleus. 0 = present, 1 = very reduced or absent. Among terrestrial carnivorans only ursids have lost the muscular process (site for insertion of tensor tympani) (Doran 1878). This process is absent in all pinnipeds also. Wozencraft (1989) incorrectly argued that absence of the muscular process is primitive.

Flynn et al. (1989:94) followed Segall (1943), who reported that ursids possess at most a very reduced muscular process. Because Segall united ursids and procyonids on the basis of the reduced muscular process Flynn et al. did not treat this feature as an ursid-pinnipedimorph synapomorphy. Wozencraft (1989:524) distinguished ursids, melines, mephitines, and lutrines from canids, procyonids, and mustelids by their small rather than large muscular processes. Wyss has rechecked Segall's carnivoran ossicle collection at the Field Museum of Natural History (Chicago) and reaffirmed that the muscular process is indeed invariably absent in bears and present in procyonids.

The derived condition, extreme reduction or loss of the muscular process on the malleus, we recognize as an ursid-pinnipedimorph synapomorphy. Because of the variation in the outgroups, this character was polarized on subsequent runs of the data.

48. *Processus gracilis* and anterior lamina of malleus. 0 = unreduced, 1 = reduced. As observed by Doran (1878), in terrestrial carnivores as in most mammals there is a slender process and a broad lamina extending between the head region and the manubrial base. In phocids, otariids and *Odobenus* the *processus gracilis* and associated lamina are greatly reduced or absent. Wozencraft (1989) reversed the polarity of this character.

Berta (1991) used the derived condition to unite all pinnipeds excluding *Enaliarctos*. Without further quantification the condition in *Enaliarctos* cannot be judged significantly different from that of other pinnipedimorphs.

49. Middle ear cavity and external auditory meatus. 0 = cavernous tissue absent, 1 = cavernous tissue developed, 2 = unique pattern of tissue development. The middle ear cavity of pinnipeds is filled by a distensible tissue thought to inflate with blood in response to increasing external pressure during diving (Repenning 1972). Phocids (exclusive of at least "*Monachus*" *schaiminslandi* show a unique (at least among pinnipeds) pattern of distribution of the cavernous tissue, thickest near the floor and roof of the middle ear cavity, thinning near the eustachian tube, across the tympanic membrane, and in the epitympanic recess (Wyss 1988b).

50. Pseudosylvian sulcus. 0 = weakly present or absent, 1 = strongly developed. In *Enaliarctos melesi* the "sylvian fossa (or more correctly pseudosylvian sulcus) is enlarged to a broad and deep crease down the side of the brain, effectively separating the cerebrum into front and back halves. Sunken within the fossa is the gyrus arcuatus primus" (Mitchell and Tedford 1973:237). According to Barnes (1979) the "Enaliarctinae" can be distinguished from other pinnipeds by their prominent pseudosylvian sulcus. He distinguished *Pteronarctos* from *Enaliarctos* by its shallower pseudosylvian sulcus (Barnes 1989). Our comparisons with additional specimens of *Pteronarctos* show that *P. goedertae* (USNM 335432) has strongly developed pseudosylvian sulci.

The pseudosylvian sulcus does not appear in amphicyonids or from the skull and endocranial cast, strongly in *Cephalogale*. The derived condition occurs in *Enaliarctos* and variably in *Pteronarctos* (Berta 1991).

#### Mandible

51. Angular (= pterygoid) process. 0 = unreduced and located near base of ascending ramus, 1 = reduced and elevated above base of ascending ramus. A well-developed angular process positioned near the base of the ascending ramus characterizes terrestrial carnivores, *Enaliarctos*, and otariids. The derived condition occurs in "monachine" phocids, odobenids, *Allodesmus*, and *Desmatophoca* (Emlong specimens).

52. Flange below ascending ramus. 0 = absent, 1 = present. A thinning and ventral extension of the posterior end of the mandibular ramus to form a bony flange below the angular process unites *Allodesmus*, *Desmatophoca*, and phocids (Berta 1991). Terrestrial carnivores and other pinnipedimorphs do not develop this flange.

53. Mandibular condyle. 0 = at or slightly above level of tooth row, 1 = well elevated above tooth row. The mandibular condyle in *Allodesmus*, *Desmatophoca*, *Pisophoca*, and *Acrophoca* is elevated above the tooth row. In most terrestrial carnivores and all other pinnipedimorphs the condyle is low.

#### Dentition

54. Deciduous dentition. 0 = unreduced, 1 = reduced. Numerous authors (e.g., King 1983) have noted that in pinnipeds the size of the

deciduous teeth is reduced.

55. Upper incisors. 0 = six, 1 = four. Living and fossil monachines have reduced the upper incisors to four from the typical pinniped and terrestrial carnivore number of six (King 1966; Muizon 1982). The apparently reduced 1' in *Allodesmus* may indicate a trend toward incisor reduction early in phocoid evolution (Wyss 1988b). This tooth is reduced or lost in the odobenines (Barnes 1989).

56. Upper incisor roots. 0 = transversely compressed, 1 = round. As noted by King (1966), the roots of the upper incisors, particularly the first two, generally are extremely compressed transversely among carnivores (including otariids, *Enaliarctos*, *Pteronarctos*, early odobenines, *Desmatophoca*, *Allodesmus*, *Cystophora*, and the Phocini). "Monachines" and *Erignathus* are characterized by roots rounder in cross-section. We recognize the derived condition as a phocid synapomorphy with a reversal in phocines.

57. 1<sup>2</sup>, transverse groove. 0 = present, 1 = absent. In otariids the first two upper incisors have a deep transverse groove (King 1983:165). This "double cusping" is also present in ursids, canids, amphicyonids, *Enaliarctos*, *Pteronarctos*, and early odobenids. The derived condition unites phocids.

58. P<sup>2</sup>. 0 = incisiform with oval cross-section, 1 = caniniform with circular cross-section. In fur seals the lateral incisor is incisiform with an oval cross-section, whereas in sea lions it is caniniform with a circular cross-section (Repenning et al. 1971). Berta and Deméré (1986) identified *Enaliarctos* and the fossil otariids *Thalassoleon* and *Pithanotaria* as sharing the primitive condition. The Otariinae (*Zalophus*, *Otaria*, *Eumetopias*, *Neophoca*, and *Phocarctos*) and Odobenidae share the derived condition.

In *Desmatophoca* 1' is procumbent and oval in cross-section (Barnes 1987). This tooth is absent from reported specimens of *Allodesmus*, although Barnes (1972:14) mentioned its procumbent roots.

59. P<sup>3</sup>, lingual cingulum. 0 = present, 1 = absent. A simple lateral incisor lacking a lingual cingulum characterizes most fossil and modern otariids (Berta and Deméré 1986). *Pithanotaria starri* shows the primitive ursid condition, in which the crown of 1' broadens posteriorly near the base and has a distinct posteromedial lingual cingulum (Repenning and Tedford 1977). The derived condition also occurs in phocids, odobenids, and *Desmatophoca* (Berta 1991). This character is usually but not always associated with "double cusping" of 1<sup>2</sup> and is a further extension of it on the lateral incisor.

60. Number of lower incisors. 0 = three, 1 = two or none. Pinnipeds have two lower incisors (King 1983); ursids, amphicyonids, and canids have three. Because the number of lower incisors is unknown for *Enaliarctos* or *Pteronarctos* we tentatively regard this character as a pinniped synapomorphy, recognizing that it might be as general as the Pinnipedimorpha.

61. Upper canines. 0 = same size as lower, 1 = larger than lower. *Disignathus* and *Imagotaria* can be distinguished from other odobenines by their upper and lower canines of similar sizes (Repenning and Tedford 1977). In contrast, odobenines (*Aivukus*, *Alachtherium*, *Gomphotaria*, *Odobenus*) have elongated upper canines, as a derived condition. *Enaliarctos*, *Pteronarctos*, otariids, and phocids share the primitive condition.

62. P<sup>1</sup>. 0 = double rooted, 1 = single rooted. The third premolar of terrestrial carnivores and *Enaliarctos* bears two separate roots. Barnes (1989) distinguished *Pteronarctos* from *Enaliarctos* by the former's bilobed posterior root. Primarily in otariids, as judged from *Pithanotaria* and *Thalassoleon* (Repenning and Tedford 1977), P<sup>1</sup> is double rooted. In odobenids, *Allodesmus*, and

*Desmatophoca* P<sup>1</sup> has a single root with two or three lobes. The double-rooted condition of this tooth among phocids represents an apparent reversal to the primitive condition (Berta 1991), or, if odobenids are monophyletic, it could be a convergence in *Desmatophoca*, *Allodesmus*, and odobenids.

63. P<sup>1</sup>, protocone shelf. 0 = present, 1 = absent. The presence of a protocone shelf on the upper carnassial has been used to distinguish *Enaliarctos* and *Pteronarctos* from all other pinnipedimorphs (Barnes 1979, 1989). The shelflike protocone is an ursid-pinnipedimorph synapomorphy (Flynn et al. 1989; Berta et al. 1989). The occurrence of a protocone shelf in *Pinnarctidion* we regard as a reversal. Because this character could not be unambiguously polarized it was excluded from the initial run of characters.

64. P<sup>2</sup>. 0 = three-rooted, 1 = three-rooted with posterior root bilobed, 2 = double rooted, 3 = single rooted. *Enaliarctos* and apparently *Pinnarctidion* (Barnes 1979:24) possess three separate roots on the upper carnassial, the primitive condition seen in terrestrial carnivorans. Three derived states may be recognized. In *Pteronarctos* the posterior root is bilobed (1). Otariids (e.g., *Thalassoleon*, *Pithanotaria*), odobenids (e.g., *Imagotaria*), and *Desmatophoca* primitively possess the double-rooted condition of this tooth (2). In other otariids, other odobenids, most phocids, and *Allodesmus* P<sup>2</sup> has only a single root (3).

65. M<sup>1</sup>. 0 = three-rooted, 1 = double-rooted, 2 = single-rooted. Although M<sup>1</sup> of *Enaliarctos meali* was originally described as having three roots, Barnes (1979) determined, in part from additional material, that it had only two roots. In *Cephalogale*, *Allocon*, and amphicyonids M<sup>1</sup> is three-rooted. Primitively in otariids this tooth is double-rooted, as in the fossil otariids *Pithanotaria* and *Thalassoleon* (Repenning and Tedford 1977).

The double-rooted (including bilobed and trilobed) condition of M<sup>1</sup> occurs in *Pteronarctos*, *Desmatophoca oregonensis* (Barnes 1989), *Pinnarctidion*, *Enaliarctos* (Barnes 1979), the archaic odobenid *Imagotaria*, and phocids. In *Desmatophoca brachycephala* and *Allodesmus* this tooth is single-rooted (Barnes 1989), as it is in most phocids and some odobenids.

66. M<sup>1-2</sup>. 0 = unreduced in size relative to premolars, 1 = reduced relative to premolars. According to Mitchell and Tedford (1973) the degree of reduction of the upper molars in *Enaliarctos* is greater than that of any known early arctoid; Berta (1991) identified it as a derived condition. Later pinnipedimorphs also show a reduced M<sup>1</sup> and reduction or loss of M<sup>2</sup> (see character 68).

67. M<sup>1-2</sup> cingulum. 0 = unreduced, 1 = reduced or absent. Archaic "musteloids," *Cephalogale*, and amphicyonids show the primitive condition, large external cingulae on the upper molars; *Enaliarctos* and other pinnipedimorphs display the derived state in which the external cingulum is reduced or absent (Mitchell and Tedford 1973).

68. M<sup>2</sup>. 0 = present, 1 = absent. The occurrence of M<sup>2</sup> varies within each of the major pinniped groups. Among walruses, M<sup>2</sup> is lacking in *Odobenus* and *Aivukus* (Repenning and Tedford 1977). In otariids, M<sup>2</sup> is lacking in *Pithanotaria* (although as noted by Repenning and Tedford this may be an artifact of preservation), *Eumetopias*, *Neophoca*, and variably in *Zalophus* (King 1983). Among phocids *Desmatophoca* and *Allodesmus* possess this tooth but phocids do not.

M<sup>2</sup> is present in all ursids and amphicyonids and variably present among archaic "musteloids" such as *Mustelictis*, *Amphictis*, *Amphicticeps*, and *Plesictis robustus* but not *P. genetoides*; see Hough (1948).

69. Lower cheek-tooth row. 0 = long, 1 = short. A short row, defined relative to the distance from P<sub>1</sub> to the ascending ramus, occurs in *Callorhinus*, *Otaria* (Berta and Deméré 1986), and *Pteronarctos* (Berta, in press). The distribution of this feature suggests it

originated separately in each taxon.

70. Lower premolars, large anterior cusp. 0 = absent, 1 = present. A large anterior cusp on the lower premolars occurs in *Enaliarctos* and *Desmatophoca* (Berta 1991). The primitive condition, lack of this cusp, characterizes *Cephalogale*, amphicyonids, and "musteloids" (Beaumont 1964; Baskin 1982). We suggest independent acquisition of this feature in *Enaliarctos* and *Desmatophoca*.

71. M<sub>1-2</sub>, trigonid and talonid. 0 = present, 1 = suppressed. The lower molars of amphicyonids, *Cephalogale*, *Enaliarctos*, and *Pteronarctos* possess a trigonid. Among all pinnipedimorphs except *Enaliarctos* and *Pteronarctos* the trigonid has been suppressed. In *Cephalogale*, a crestlike entoconid and distinct hypoconid occur, whereas in *Enaliarctos* and *Pteronarctos* only the hypoconid is present, an intermediate condition (Mitchell and Tedford 1973; Berta, in press). In all other pinnipedimorphs the talonid has been suppressed.

72. M<sub>1</sub>, metaconid. 0 = present, 1 = reduced or absent. In amphicyonids the metaconid is variable, being large (*Daphoenus*, *Daphoenocyon*) or reduced (*Daphoenictis*) (Hunt 1974). In *Cephalogale* the metaconid is subequal to the paraconid but is progressively reduced through the lineage (Beaumont 1965:6, 33). *Enaliarctos* is characterized by a greatly reduced metaconid (Mitchell and Tedford 1973), and this cusp is suppressed in all pinnipeds except *Enaliarctos* and *Pteronarctos* (Berta, in press).

73. M<sub>2</sub>. 0 = present, 1 = absent. All pinnipedimorphs except *Enaliarctos* and *Pteronarctos* lack M<sub>2</sub> (Berta 1991). This tooth is consistently present among terrestrial carnivorans, in one species of *Desmatophoca*, *D. oregonensis* (Berta, in press), and perhaps in *Pithanotaria* (see Repenning and Tedford 1977:58).

74. M<sub>3</sub>. 0 = present, 1 = absent. The third lower molar is absent in all pinnipedimorphs but present in *Amphicyonodon*, *Pachycynodon*, *Allocon*, *Cephalogale*, and amphicyonids. Tedford (1976) united mustelids, procyonids, and phocids (Mustelida) partly on the basis of the loss of M<sub>3</sub>. He interpreted the loss of M<sub>3</sub> in "otarioids" as independent. We interpret this tooth to have been lost independently among "musteloids" and pinnipedimorphs.

75. Cheek tooth crowns. 0 = compressed, 1 = bulbous. Bulbous cheek-tooth crowns characterize *Allodesmus*, *Desmatophoca*, and *Dusignathus* (Barnes 1989) as well as phocids.

#### Axial Skeleton

76. Cervical vertebrae, transverse processes and neural spines. 0 = large, 1 = small. Howell (1929:20) noted that well-developed transverse processes and neural spines on the cervical vertebrae characterize otariids, whereas the cervical vertebrae are smaller and the transverse processes less stout in phocids. The cervical vertebrae of *Odobenus* more nearly resemble those of phocids in their small size (see comments below). The primitive condition characterizes ursids (Davis 1964:78). The condition in *Enaliarctos* is unknown. The derived condition is thus either a synapomorphy uniting odobenids and phocids, with *Allodesmus* representing a reversal, or originated independently in odobenids and phocids.

77. Cervical vertebrae. 0 = larger than thoracic and lumbar, with spinal canal less than one-half the diameter of the centrum, 1 = smaller than thoracic and lumbar, with spinal canal nearly as large as centrum. *Odobenus* and phocids share cervical vertebrae that are smaller than the thoracics and lumbar (Fay 1981:10). In otariids the cervical vertebrae are larger than the thoracics, a condition we regard as primitive on the basis of outgroup comparison. The condition in *Enaliarctos* is unknown (Berta and Ray 1990). In *Allodesmus* the cervical vertebrae appear larger than the thoracics (Mitchell 1966:8, pl. 7).

Like the previous character, this one is an odobenid + phocid

synapomorphy, with *Allodesmus* representing a reversal, or a feature independently derived in odobenids and phocids.

78. Atlas, vertebrarterial (= transverse) foramen. 0 = visible in posterior view, 1 = visible in dorsal view. Among phocids two conditions occur (King 1966). In "*Monachus*" *monachus* the foramen is visible only in posterior view, as in most terrestrial carnivorans (except canids), otariids, the fossil odobenid *Imagotaria*, *Allodesmus*, and phocines. In *Mirounga* and lobodontine phocids, the transverse foramen is visible dorsally. In "*Monachus*" *tropicalis* and *Odobenus* the foramen is partially visible in dorsal view (Wyss 1988).

79. Thoracic vertebrae, neural spines. 0 = high, 1 = low. In contrast to phocids and *Odobenus*, which have low neural spines, otariids show high neural spines on the thoracic vertebrae (King 1983:156). Ursids, *Enaliarctos*, and *Allodesmus* possess high neural spines (Davis 1964; Berta and Ray 1990; Mitchell 1966:10, pl. 10).

80. Lumbar vertebrae, transverse processes. 0 = short, 1 = long. Otariid lumbar vertebrae show small transverse processes and closely set zygapophyses, while those of phocids show larger transverse processes and more loosely fitting zygapophyses (King 1983:156). In *Odobenus*, as in the Phocidae, the transverse processes are two or three times as long as wide (Fay 1981:10), whereas in otariids these processes are about as long as wide. In ursids the transverse processes are relatively short (Davis 1964). The transverse processes of the lumbar vertebrae of *Allodesmus* (Mitchell 1968: pl. 11) and *Enaliarctos* (Berta and Ray 1990) are longer than wide. We interpret the derived condition to have arisen independently in *Enaliarctos* and in a group including odobenids, *Allodesmus*, and phocids or as primitive for pinnipedimorphs with a reversal in otariids.

81. Lumbar vertebrae. 0 = six, 1 = five. Five lumbar vertebrae are present in most pinnipeds, although six are more usual in walrus (Fay 1981; King 1983:154). In *Ursus* the number of lumbar is six in 79% of specimens and five in the remaining 21% (Davis 1964:74, table 9). *Enaliarctos* had six lumbar vertebrae (Berta and Ray 1990), whereas *Allodesmus* had five (Mitchell 1966).

As we have coded this character, it diagnoses the pinnipeds with a reversal in walrus.

#### Pectoral Girdle and Forelimb

82. Scapula, hooklike process of teres major. 0 = absent, 1 = present. This process is common to all phocids except *Mirounga* and "*Monachus*." The shape of the caudal angle in *Mirounga* and "*Monachus*" more nearly resembles that in odobenids, otariids, and *Allodesmus*. Hence we regard the hooklike process as an apomorphy of phocines and lobodontines (Wyss 1988b).

83. Scapula, acromion process. 0 = knoblike, 1 = reduced. The acromion process is reduced in the phocines. A knoblike acromion occurs in ursids, *Allodesmus*, *Odobenus*, otariids, and *Enaliarctos* and is therefore likely primitive for pinnipeds (Wyss 1988b).

84. Scapula, scapular spine. 0 = unreduced, 1 = slightly reduced, 2 = very reduced. Phocids exemplify three distinctive patterns of scapular spine development (Wyss 1988b:17): a strongly developed spine that may extend to the vertebral scapular border, as in phocines, an intermediate condition in which the spine reaches or nearly reaches the scapular margin but is less prominent than in phocines, a condition seen in "*Monachus*" and *Mirounga*, and spine extremely reduced, serving only as a support of the acromion process, as in lobodontines. The scapular spine is large and well developed in ursids (Davis 1964) and amphicyonids, e.g., *Daphoenocyon* (Hough 1948).

85. Supraspinous fossa. 0 = slightly larger than infraspinous fossa, 1 = considerably larger than infraspinous fossa. A large supraspinous fossa is a constant feature in otariids, *Odobenus*, *Allodesmus*, and *Enaliarctos* (Mitchell 1966; Bisaillon and Pierard 1981; Berta and Ray 1990: fig. 3). In relation to the infraspinous fossa, the supraspinous fossa tends to become substantially reduced, particularly among the phocines. As a result the scapula of these taxa could be interpreted as more closely resembling that typical of terrestrial carnivorans than that of any other pinniped (Wyss 1988b). Berta and Ray (1990) identified the derived condition as a pinnipedimorph synapomorphy, as it is considered here. It is one of a very few possible otarioid synapomorphies (accepting a monophyletic Monachinae and convergence between that group and "otarioids"), but is contradicted by overwhelming evidence of pinniped monophyly.

86. Secondary spine of scapula. 0 = absent, 1 = present. A ridge subdividing the supraspinous fossa is present in otariids (King 1983) but not in walrus or phocids (English 1975). The condition of the spine in *Enaliarctos*, *Pteronarctos*, and *Allodesmus* is unknown. Accordingly, we regard the secondary scapular spine as an otariid synapomorphy.

87. Greater and lesser tuberosities of humerus. 0 = unenlarged, 1 = enlarged. In pinnipeds, the greater and lesser tuberosities are very prominent relative to the primitive carnivoran condition, although the greater is considerably more enlarged in otariids and the lesser more enlarged in phocids (Howell 1929). *Enaliarctos* has enlarged humeral tuberosities (Berta and Ray 1990), thus the derived condition is a pinnipedimorph synapomorphy.

88. Deltopectoral crest of humerus. 0 = not strongly developed, 1 = elongated and strongly developed, 2 = short and strongly developed. Pinnipedimorphs are distinguished from terrestrial carnivorans by having strongly developed deltopectoral crests. In "monachine" phocids, otariids, odobenids, and *Allodesmus* the deltoid crest is elongated, extending two-thirds to three-quarters the length of the shaft at which point the crest and shaft merge smoothly. In phocines the deltoid crest extends less than one half the length of the shaft and ends abruptly, in lateral view nearly overhanging the shaft. The insertion of the pectoralis is then more proximally restricted. The shorter, more abruptly ending crest in phocines does not represent the generalized phocid condition but is more likely a secondary derivation (Wyss 1988b), a conclusion supported by our analysis.

89. Supinator ridge of humerus. 0 = well developed, 1 = absent or poorly developed. The supinator ridge, absent in otariids, odobenids, and *Allodesmus* (Repenning and Tedford 1977; Mitchell 1968) is well developed in terrestrial carnivorans, including ursids, procyonids, some mustelids (Davis 1964), and *Enaliarctos* (Berta and Ray 1990). As noted by King (1966), this ridge is strongly developed in phocines and absent in "monachines."

90. Humerus. 0 = long and slender, 1 = short and robust. Following Wyss (1989), Berta and Ray (1990) identified a short, robust humerus as a pinnipedimorph synapomorphy. In terrestrial carnivorans, the humerus is longer and more slender than that in pinnipeds (English 1975:90).

91. Entepicondylar foramen. 0 = present, 1 = absent. An entepicondylar (= supracondylar) foramen is usually found in phocines but not in "monachines" (some exceptions have been reported among fossil "monachines") or other pinnipeds (King 1983:157). An entepicondylar foramen is absent in *Enaliarctos*. It is present in *Ailuropoda* and *Tremarctos* but otherwise absent in the Ursidae. It is large in *Potamotherium* (Savage 1957) and amphicyonids. Absence of an entepicondylar foramen is the ancestral pinnipedimorph condition (Berta and Ray 1990). Uncertainties

in polarity notwithstanding, absence of this foramen cannot effectively be used to diagnose "otarioids" (Barnes 1989) because this condition also likely persists ancestrally to phocids.

92. Olecranon fossa. 0 = deep, 1 = shallow. The humerus of all pinnipediforms including *Enaliarctos* is characterized by a shallow olecranon fossa. The olecranon fossa of terrestrial carnivorans is deep (Berta and Ray 1990). Hence we regard this feature as a pinnipediform synapomorphy.

93. Diameter of humeral trochlea. 0 = same as diameter of distal capitulum, 1 = considerably larger than diameter of distal capitulum. Repenning and Tedford (1977) used this feature to distinguish odobenids from otariids. In odobenids the anteroposterior diameter of the trochlea is considerably larger than that of the distal capitulum. In *Allodesmus* the trochlea is approximately the same diameter as the distal capitulum. In *Erignathus* and the Phocini the trochlea is larger than the distal capitulum. From this distribution, we interpret this character as having arisen independently in the Odobenidae and Phocinae, then having been lost in *Cystophora*.

94. Olecranon process. 0 = knoblike and unexpanded, 1 = laterally flattened and posteriorly expanded. The pinniped condition, in which the olecranon process is laterally flattened and posteriorly expanded, is not seen elsewhere in the Carnivora or in other aquatic mammals (Wyss 1989). As identified by Berta and Ray (1990), the derived condition unites pinnipeds; it does not occur in *Enaliarctos*.

95. Radius. 0 = convexly arched and unexpanded, 1 = markedly flattened anteroposteriorly, with expanded distal half. The derived condition characterizes a group at least as inclusive as the Pinnipedia (Howell 1929; King 1983; Wyss 1988a) and it may be found to characterize the Pinnipediformes once a *Pteronarctos* radius becomes known. It is approached slightly in *Potamotherium* (Savage 1957). In terrestrial carnivorans, the radius is convex and bent in a sigmoid curve in the lateral plane.

96. Pronator teres process. 0 = absent, 1 = present, proximal, 2 = present, distal. Howell (1929) described a well-defined "pronator teres process" on the shaft of the medial side of the radius in pinnipeds. This feature is not strongly marked among terrestrial carnivorans except *Potamotherium* (Savage 1957, fig. 24).

Repenning and Tedford (1977) used the position of the pronator teres process to distinguish otariids, in which the process is more proximal, from odobenids, in which it is more distal. A more distal pronator teres process also characterizes "*Monachus*," *Mirounga*, and the fossil lobodontines *Acrophoca*, *Homophoca*, and *Piscophoca*; in *Allodesmus*, phocines, and extant lobodontines the pronator teres process is positioned proximally.

We consider the pronator teres process a pinnipediform synapomorphy. State 1, a proximally positioned process, is common to *Enaliarctos* and otariids. A more distal process, state 2, unites odobenids and phocids primitively, with the condition in *Allodesmus*, lobodontines, and phocines representing reversals.

97. Distally projecting ledge on cuneiform. 0 = absent, 1 = present. King (1966) considered the distally projecting process (palmar process) that arcs over the palmar surface of the fifth metacarpal head as distinctively phocine. This process is absent in otariids, odobenids (except *Imagotaria*), *Allodesmus*, "monachines," and other phocids. Terrestrial carnivorans lack a palmar process (Yalden 1970).

98. Manus. 0 = central digits (II-IV) more strongly developed, 1 = digit I emphasized, digits II-V progressively smaller. In the hand of pinnipediforms digit I (metacarpal I and proximal phalanx) is elongated, whereas in other carnivorans the central digits are the most strongly developed (Wyss 1987:18, fig. 6; Wyss 1989). The manus of pinnipediforms is ectaxonic (Brown and Yalden 1973),

the digits of the pollical side being the longest and those of the ulnar side being smallest (English 1975:110). Terrestrial carnivorans show a more symmetrically arranged mesaxonian manus with digit III the longest, the second and fifth the next longest, and the pollex the shortest (English 1976:3, table 1).

Berta and Ray (1990) considered digit length individually and collectively (i.e., progressive decrease in size of digits I-V) as separate characters.

The derived condition occurs in *Enaliarctos* (Berta and Ray 1990), so we interpret it as a pinnipediform synapomorphy.

99. Metacarpal I, pit or rugosity. 0 = absent, 1 = pit present, 2 = rugosity present. According to Barnes (1989) the pit or rugosity on the proximal dorsal surface of metacarpal I for attachment of the pollicle extensor muscle distinguishes odobenids from other "otarioid" pinnipeds. He identified the imagotarines *Imagotaria* and *Pliopedia* as bearing a pit, the odobenines *Aivukus* and *Odobenus* as bearing a rugosity. Repenning and Tedford (1977) found the condition in *Dusignathus* similar to that in *Imagotaria*. There is no pit or rugosity in *Allodesmus*, otariids (Mitchell 1968), or phocids (Murie 1871). Therefore we interpret the pit or rugosity on metacarpal I as an odobenid synapomorphy.

100. Metacarpal heads. 0 = keeled with trochleated phalangeal articulations, 1 = smooth, with phalanges flat, articulations hingelike. King (1966) noted that in phocines (as in most terrestrial mammals) a longitudinal ridge divides the distal and palmar surfaces of the metacarpal head. Coinciding with this arrangement, the proximal articulation surfaces of the proximal phalanges are marked by a deep notch on their palmar margins accommodating these metapodial ridges. By contrast, in other phocids the metacarpal heads are smooth and the metacarpophalangeal and interphalangeal articulations are flatter, broader, and hingelike. The "monachine" configuration closely resembles that seen in otariids, odobenids, and *Allodesmus* (Wyss 1988b). As judged from *Enaliarctos* (Berta and Ray 1990), the ancestral pinnipediform condition is one in which the metacarpal heads are keeled and the phalangeal articulations are trochleated. The phocine condition thus represents a reversal to the primitive condition.

101. Metacarpal I and II. 0 = approximately equal in size, 1 = metacarpal I longer. Pinnipeds except phocines are characterized by having the first metacarpal greatly elongated and thicker in comparison to metacarpal II (King 1966; Wyss 1988b: fig. 5). Among terrestrial carnivorans these elements are approximately equal in size. Therefore we regard the phocine condition as a reversal to the primitive condition.

102. Digits, cartilaginous extensions. 0 = absent, 1 = present. Cartilaginous rods distal to each digit serve to support an extension of the flipper border; they occur and are long on both the fore- and hindflippers of otariids. Short cartilaginous extensions are present in walrus (Fay 1981) and *Allodesmus* (Mitchell 1966:15). King (1969) reported diminutive cartilaginous extensions in the phocid *Ommatophoca* and suggested they probably exist in *Hydruga* as well.

As Wyss (1987:23) wrote, "it seems conceivable that the primitive pinniped flipper was approximated by that of the walrus (short cartilaginous extensions present), that in otariids with their emphasis on forelimb propulsion these extensions have become greatly elongate, and that in phocids with their emphasis on hindlimb propulsion the extensions have become secondarily lost."

The probable development of cartilaginous extensions in *Enaliarctos* (as judged from the flat distal articular surface of the terminal phalanges on both hands and feet) implies they are primitive for pinnipediforms.

103. Foreflipper claws. 0 = long, 1 = short. As noted by King

(1966) the fore- and hindflippers of phocines are characterized by well-developed claws; in other phocids the claws tend to be poorly produced. In otariids and *Odobenus* the claws of the manus are reduced, as was probably the case in *Allodesmus*. As long claws on the manus are found among terrestrial carnivores, we interpret them as primitive.

104. Manus, digit V, intermediate phalanx. 0 = unreduced, 1 = strongly reduced. King (1966) distinguished "monachines" from phocines by the strong reduced fifth intermediate phalanx of their manus. Yet this condition occurs in all other pinnipeds for which the region is known. Wyss (1988b, 1989) and Berta and Ray (1990) listed the derived condition as a synapomorphy of pinnipeds with a reversal in phocines.

105. Pes. 0 = central digits elongated, 1 = digits I and V emphasized. Pinnipedimorphs including *Enaliarctos* have elongated digits I and V (metatarsal I and proximal phalanx) in the pes whereas in other carnivores the central digits are the most strongly developed in the pes (Wyss 1987:18, fig. 6; Wyss 1988a; Berta and Ray 1990).

106. Metatarsal III. 0 = approximately equal to the others; 1 = much shorter. Among "monachines" and *Cystophora* the third metatarsal is considerably shorter than the others (Wyss 1988b, fig. 7). In other pinnipeds and terrestrial carnivores the metatarsals are approximately equal. Thus the "monachine" condition is derived, with the lengthening of this element among phocines (exclusive of *Cystophora*) a reversal to the primitive condition, or a convergence in "monachines" and *Cystophora*.

107. Hindflipper claws. 0 = unreduced, 1 = reduced, 2 = markedly reduced. As noted by King (1966) reduced claws on the hindflipper are common among "monachines." Because the hindlimb claws (at least on the central three digits) of other pinnipeds tend to be strongly developed, Wyss (1988b) interpreted this condition as a potential "monachine" synapomorphy. Terrestrial carnivores show the primitive condition, well-developed claws on both the manus and pes.

108. Pes. 0 = short, rounded metatarsal shafts with rounded heads, associated with trochleated phalangeal articulations. 1 = long, flattened metatarsal shafts with flattened heads, associated with nontrochleated, hingelike phalangeal articulations. Correlated with the morphology of the hand is that of the foot. Pinnipeds (except phocines) are characterized by relatively long, flattened metatarsal shafts with flattened heads associated with smooth, hingelike phalangeal articulations (Wyss 1988, 1989). The ancestral pinnipedimorph condition, seen in *Enaliarctos*, resembles that of terrestrial carnivores, in which the metatarsal heads are keeled and associated with trochleated phalangeal articulations (Berta and Ray 1990). Therefore we regard phocines as having reverted to the primitive condition.

109. Pubic symphysis. 0 = fused, 1 = unfused. In terrestrial carnivores the pubic symphysis forms a fully ossified union, whereas in pinnipedimorphs only a ligament binds adjoining bones (Savage 1957). Berta and Ray (1990) identified the derived condition as occurring in all pinnipeds except *Enaliarctos*.

110. Ilium. 0 = relatively long, 1 = short. Compared with that of terrestrial mammals, the pinnipeds' pelvis has a shortened ilium and an elongated ischium and pubis (King 1983; see Tarasoff 1972:340, table 4 for comparisons among *Canis*, *Lutra*, *Pagophilus* and *Zalophus*). Berta and Ray (1990) identified the derived condition as a synapomorphy uniting pinnipedimorphs.

111. Ilium. 0 = anterior termination simple, 1 = strongly everted, laterally excavated anteriorly. Living phocines except *Erignathus* are characterized by a lateral eversion of the ilium accompanied by

a deep lateral excavation (King 1966). Terrestrial carnivores and other pinnipedimorphs possess the primitive condition in which the ilium is not strongly excavated laterally.

112. Insertion for ilial psoas muscle. 0 = on femur, 1 = on ilium. In all phocids the psoas major muscle inserts on the ventral edge of the ilium. In all other pinnipeds and terrestrial carnivores this muscle inserts on the lesser trochanter of the femur (Muizon 1982, fig. 183). The derived condition is a phocid synapomorphy.

113. Separate foramen in innominate for obturator nerve. 0 = absent, 1 = present. A separate foramen for passage of the obturator nerve, the obturator foramen, occurs in *Thalassoleon mexicanus* and *Allodesmus*, variably in the arctocephaline otariids and *Odobenus* (Repenning and Tedford 1977; Mitchell 1966; Fay 1982). Phocids (exclusive of "*Monachus*" *schauinslandi*, *Piscophoca*, and *Acrophoca*) lack this foramen (Repenning and Ray 1977; Muizon 1981). The absence of the foramen in terrestrial carnivores and *Enaliarctos* suggests that its absence in phocids (except "*M.*" *schauinslandi*, *Piscophoca*, and *Acrophoca*) represents a reversal; a high degree of variability, however, makes this difficult to judge.

114. Ischial spine. 0 = unenlarged, 1 = large. A large dorsally directed ischial spine is present in phocids and odobenids. According to King (1983:160, fig. 6.24), muscles attached to this spine help elevate the hindflippers and produce the phocids' characteristic posture.

Ursids have a small ischial spine, the primitive condition (Davis 1964). The ischial spine is small in *Allodesmus* also (Mitchell 1966: pl. 20). Accordingly, this feature is most parsimoniously interpreted either as a synapomorphy uniting odobenids and phocids [except *Homiphoca* (Muizon and Hendey 1980, fig. 12) and *Allodesmus*] or as independently derived in odobenids and phocids.

115. Fovea for teres femoris ligament (= lig. capitis femoralis). 0 = present and well developed, 1 = strongly reduced or absent. Pinnipeds share the derived condition of the position of the fovea on the head being barely visible and the ligament lacking (King 1983:161). *Enaliarctos* retains the primitive condition, a well-defined pit on the head for the teres femoris ligament (Berta and Ray 1990).

116. Lesser femoral trochanter. 0 = present, 1 = very reduced or absent. According to King (1983:161) "the lesser trochanter is present only as a small knob distal to the head in otariids and is absent in phocids." *Allodesmus* has a rugose raised area representing the lesser trochanter (Mitchell 1966), and *Odobenus* has a similar scar. The lesser trochanter is extremely well developed in the fossil walrus *Imagotaria*, more so than in living otariids, and contrasting even more strongly with the living walrus (Repenning and Tedford 1977:38). Since walrus primitively possess a distinct lesser trochanter, apparently its reduction or loss occurred independently in later walrus and the phocid clade (*Allodesmus* + phocids), unless it reappeared as an autapomorphy in *Imagotaria*.

117. Greater femoral trochanter. 0 = small and rounded, 1 = large and flattened. The derived condition is a pinniped synapomorphy, as Berta and Ray (1990) identified it in all pinnipedimorphs except *Enaliarctos*. In terrestrial carnivores and *Enaliarctos* the greater trochanter is separate from the lateral femoral border rather than being broadly continuous with it as in pinnipeds.

118. Medial inclination of condyles. 0 = slight, 1 = strong. The angle of inclination of the femoral condyles is the angle formed across the condyles to a line perpendicular to the shaft (see Tarasoff 1972: table IV for comparisons). A small angle of inclination (approximately 10°) was noted for *Potamotherium* (Savage 1957) and is the common condition for terrestrial carnivores. With this femoral specialization is associated an increased angle of slope on

the condyles of the tibia. Berta and Ray (1990) used the derived condition to diagnose pinnipedimorphs including *Enaliarctos*.

119. Trochanteric fossa of femur. 0 = unreduced, 1 = reduced or absent. According to King (1983), the trochanteric fossa is small but present in phocines and otariids but absent in "monachines." But, as Muizon (1981) has pointed out, some "monachines" (i.e., *Homiphoca* and *Piscophoca*) have a trochanteric fossa. The primitive condition, a deep trochanteric fossa, is present among ursids (Davis 1964), *Potamotherium* (Savage 1957), and *Enaliarctos* (Berta and Ray 1990). The derived condition unites otariids, odobenids, *Allodesmus*, and phocids (i.e., the Pinnipedia, with reversals characterizing the taxa noted above).

120. Patella. 0 = flat, 1 = conical. According to King (1983:161), the patella of phocids is flatter, that of otariids and walruses, more conical. The flat patella of the fossil walrus *Imagotaria* indicates that the flattened condition may be primitive for walruses. *Allodesmus* possesses a conical patella (Mitchell 1966: pl. 20). Ursids are characterized by a relatively flat patella (Davis 1964). Since the patella of *Enaliarctos* is conical, this condition may be primitive for pinnipeds (Berta and Ray 1990), with the flattened condition representing a reversal, occurring once among early walruses and once among phocids.

121. Post-tibial fossa. 0 = weak, 1 = strong. The post-tibial (= intercondyloid) fossa is more strongly developed in phocines than in "monachines" (King 1966). This fossa is shallow in otariids, *Odobenus*, *Allodesmus*, *Enaliarctos*, and most terrestrial carnivorans. Hence, the derived condition is a phocine synapomorphy.

122. Tibia and fibula. 0 = unfused, 1 = fused proximally. The tibia and fibula are fused at their proximal ends in otariids (except *Callorhinus* and the fossil *Thalassoleon mexicanus*) and phocids (except "*Monachus*" *schaininslandi*). In walruses these elements are separate, even in old animals (King 1983:161). In *Callorhinus* the tibia and fibula are unfused (Lyon 1937). *Thalassoleon macnallyae* (in contrast to *T. mexicanus*) has a proximally fused tibia and fibula (Repenning and Tedford 1977). These elements are unfused in *Allodesmus* (Mitchell 1966), *Enaliarctos* (Berta and Deméré 1986), and terrestrial carnivorans. This distribution suggests that the ancestral pinnipedimorph condition is unfused (Berta and Ray 1990).

123. Calcaneal secondary shelf. 0 = absent, 1 = present. All living otariids possess a well-developed secondary shelf of the sustentaculum (Robinette and Stains 1970). According to Repenning and Tedford (1977:39), this shelf is not seen in *Imagotaria*. Nor have we seen it in *Odobenus*. It is "essentially lacking" in the fossil otariid *Thalassoleon mexicanus* and only slightly developed in *Hydrarctos lomastensis* (Muizon 1978). Thus the derived condition is an autapomorphy of otariids above the level of *Thalassoleon*.

124. Calcaneal tuber. 0 = long, 1 = short. In terrestrial carnivorans, when the calcaneum is in articulation with the astragalus the calcaneal tuber extends far proximal of the astragalus head. This also tends to be the case in otariids, but in phocids the calcaneal tuber is shortened and projects posteriorly only as far as the process of the astragalus. Similarly, in odobenids and *Allodesmus* the calcaneal tuber is short and extends only slightly beyond the head (from Mitchell 1966: pls. 21, 22). In agreement with Wyss (1987), Berta and Ray (1990) identified the derived condition as a synapomorphy uniting odobenids, *Allodesmus*, and phocids.

125. Medial process on calcaneal tuber. 0 = absent, 1 = present. Repenning and Tedford (1977) noted that walruses are characterized by a prominent tuberosity on the medial side of the calcaneal tuber. This process is absent in other pinnipedimorphs and terrestrial carnivorans. Hence we interpret the derived condition as an

odobenid synapomorphy.

126. Caudally directed process (calcaneal process) of astragalus. 0 = absent, 1 = present, 2 = well developed. The phocid astragalus is distinguished by a strong caudally directed process over which the tendon of the flexor hallucis longus passes. This arrangement prevents anterior flexion of the foot, resulting in seals' inability to bring their hindlimbs forward during locomotion on land. In the living walrus there is at least a tendency toward development of a calcaneal process (better developed in *Imagotaria*; Repenning and Tedford 1977), and *Allodesmus* appears to be similar (see Mitchell 1966: pls. 21, 22). A calcaneal process is absent in terrestrial carnivorans, *Enaliarctos*, and otariids (Howell 1930).

We interpret presence of a calcaneal process on the astragalus as a multitaste character. An intermediate condition (1) occurs in walruses and *Allodesmus*; the second condition (2) is unique to phocids.

127. Baculum. 0 = unenlarged, 1 = enlarged. Scheffer and Kenyon (1963), Wyss (1987), and Berta and Ray (1990) showed odobenids, phocids, and *Allodesmus* to share the derived condition of large bacula; otariids retain the primitive unenlarged condition.

#### Soft-Anatomical and Behavioral

128. Testes. 0 = scrotal, 1 = abdominal (i.e., inguinal). The testes of otariids and terrestrial carnivorans lie outside the inguinal ring. In contrast, in phocids and *Odobenus* the testes are inguinal (Harrison et al. 1952; Fay 1981, 1982; Davis 1964).

129. Copulation. 0 = terrestrial, 1 = aquatic. *Odobenus* and phocids (except *Mirounga*) copulate in the water, whereas otariids and other carnivorans copulate on land.

130. Pelage. 0 = abundant, 1 = sparse, 2 = secondary hairs absent. Berta and Deméré (1986) used lack of underfur as a derived condition to diagnose sea lions. Sparse underfur is also diagnostic of *Odobenus* and phocids (Scheffer 1958), in which it evolved independently from sea lions. Secondary hairs occur in otariids and the majority of phocids but are virtually absent in "*Monachus*," *Mirounga*, and *Odobenus* (Scheffer 1964; Fay 1982).

131. Natal coat. 0 = black, 1 = gray or white. Phocids exclusive of "*Monachus*" and *Mirounga* have a first pelage paler than that of otariids, odobenids, and most terrestrial carnivorans, a condition that Wyss (1988b) interpreted as a potential synapomorphy uniting phocines and lobodontines.

132. Primary hair. 0 = medullated, 1 = nonmedullated. Scheffer (1964) observed that the primary hairs of otariids have a medulla but those of phocids and *Odobenus* do not. Since medullated hair has been documented for *Canis* and *Mustela* (Noback 1951), the derived condition has been interpreted as a synapomorphy uniting phocids and *Odobenus* (Wyss 1987).

133. Mystacial whiskers. 0 = smooth, 1 = beaded. Beaded mystacial whiskers diagnose all phocids except "*Monachus*," *Erignathus* (Wyss 1988b), *Ommatophoca*, and *Hydrurga* (Ling, pers. comm.), which have retained or reverted to the primitive smooth condition.

134. Molt. 0 = cornified tissue and hair do not form sheets, 1 = cornified tissue and hair form sheets during molt. As noted by Wyss (1988b), an unusual pattern of molting characterizes *Mirounga* and "*Monachus*" *schaininslandi* (only species of that genus whose molt has yet been examined). In these seals, the primary hairs become fused to the stratum corneum so that when the pelage is shed it forms large continuous patches held together by this thin layer of cornified epidermal tissue. Wyss interpreted this feature as an apomorphy of these two species.

135. Pelage units. 0 = arranged alternately, 1 = spaced uniformly. Scheffer (1964) pointed out that in *Odobenus* and phocids the pelage units are arranged in groups of two to four or in rows. In otariids the pelage units are uniformly spaced. Because the pelage units of *Ursus* and *Canis* are arranged alternately (Mejere 1884), Wyss (1987:10) considered their uniform arrangement in otariids a synapomorphy of that family.

136. Subcutaneous fat. 0 = thin, 1 = thick. Tarasoff (1972) noted that walruses and phocids are characterized by thick layers of subcutaneous fat. These layers are less well developed in otariids and lacking in other terrestrial carnivores, including lutrines.

137. Mammary teats. 0 = four, 1 = two. Ursids (Davis 1964), otariids, and *Odobenus* have two pairs of nipples, whereas phocids except "*Monachus*" and *Erignathus* have only one pair, thought to correspond to the posterior pair of other pinnipeds (King 1983).

138. Grooming. 0 = extensive, 1 = lacking. Associated with sparse pelage is the lack of grooming observed in walruses and phocids (Tarasoff 1972). Since grooming is recorded for lutrines we tentatively interpret lack of grooming as the derived condition.

139. External pinnae. 0 = present, 1 = absent. *Odobenus* and phocids lack external ear pinnae, the presence of which characterizes otariids and other terrestrial carnivores.

140. Sweat-duct orifice position. 0 = distal, 1 = proximal. In the adult walrus and phocids sweat ducts open proximal to the opening of the sebaceous glands. By contrast, in otariids the sweat duct is more distal (Ling 1965, Fay 1982).

141. Venous system. 0 = hepatic sinus uninflated, caval sphincter absent, interventricular sinus small, posterior vena cava single, 1 = hepatic sinus inflated, caval sphincter well developed, interventricular sphincter large, posterior vena cava duplicate, route for hindlimbs gluteal. Walruses and phocids share the specialized venous system outlined above (Fay 1981). In contrast, otariids have a less specialized venous system that more closely approximates the typical mammalian pattern. Wyss (1987) used the derived condition to unite *Odobenus* and the phocids.

142. Pericardial plexus. 0 = poorly developed, 1 = well developed. Another structure of the venous system, a well-developed pericardial plexus, distinguishes phocids exclusive of "*Monachus*" *schauinslandi* from otariids and *Odobenus* (Harrison and Tomlinson 1956; King and Harrison 1961; King 1977; Fay 1981).

143. Trachea. 0 = bifurcation of bronchi anterior, 1 = bifurcation of bronchi posterior. Fay (1981) and King (1983: fig. 9.2) observed that in the walrus and phocids the trachea divides into the two primary bronchi immediately outside the lung. A similar condition occurs in ursids and canids. By contrast, in otariids the bifurcation is more anterior, at the level of the first rib, and the two elongated bronchi run parallel until they diverge to enter the lungs dorsal to the heart. Hence the derived condition represents one of the very few synapomorphies of the Otariidae.

## APPENDIX 2

Diagnostic characters for the nodes and terminal taxa in Figure 2 are summarized below according to conventions used by Gauthier et al. (1988). These diagnoses were obtained from the consensus topology by means of the "describe-tree" option in PAUP version 3.0s (Swofford 1991). Synapomorphies are placed at the level(s) of

generality at which they are observed. Some characters may be of a more general distribution; these are placed in brackets. Reversals are designated by a minus sign preceding the character number. Ambiguous character assignments (including convergences) are designated by an asterisk following the character number. Only terminal taxa that could be autapomorphously characterized are listed.

Pinnipedimorpha: [9], [10], [11], 15, 17\*, 19\*, 25, 27, [31], 40, 43, 47\*, 48, [49], [54], [60], 65\*, 66, 72, 80\*, 85\*, 87, 88, 90, 91\*, 92, 96\*, 98, 101\*, 103\*, 104\*, 105, 110, 118, 120\*

*Enaliarctos*: 50, 70\*

Pinnipediiformes: 3\*, 9, 10, 14, 24, 64\*, [81], 89\*, [94], [95], 100\*, 108\*, [109], 113\*, [115], [117], 119\*

*Pteronarctos*: 69\*

Pinnipedia: 7\*, 8\*, 16\*, 30, 59, 63\*, 64\* (1 to 3), 71, 73\*, 81, 94, 95, 115, 117, 119

Otariidae: 4, 12\*, 17\* (1 to 3), -80, 86, 135, 143

*Thalassoleon*: 64

Unnamed node (*Arctocephalus* + *Callorhinus* + Otariinae): 62\*, 65\* (1 to 2), 123

Unnamed node (*Arctocephalus* + Otariinae): -113, 122\*

*Callorhinus*: 69\*

Otariinae: 58\*, 130\*

Phocomorpha: 26\*, 32, 34, 37\*, 42, 46, 51, 57\*, 76\*, 77\*, 79\*, 96 (1 to 2), 107\*, [114], [116], 124, 126, 127, 128, 129, 130\* (0 to 2), 132, 136, 138, 139, 140, 141

Phocidae: 1\*, 2\*, -3, 5, 6\* (1 to 2), 13, -16, 22, 24 (1 to 2), 26 (1 to 2), 35, 39\*, 45\*, 52, 53\*, 65\* (1 to 2), 75, 133\*, 137\*, 142

*Allodesmus*: 26 (2 to 1), 39\* (1 to 2), 62\*, -73, -76, -77, -79, -114

*Desmatophoca*: 62\*, 64 (3 to 2), 70\*

*Pinnarctidion*: -7, -19, -63, 64\* (3 to 0), 65\* (2 to 1), 68\*, -75

Phocidae: 6 (2 to 1), 12\*, 17\* (1 to 2), 20, 23, 28, 29, 33, 37\* (1 to 2), 39\* (1 to 2), 41, -45, -53, 56\*, 68\*, -102, 112, -113, -120, 122\*, 126 (1 to 2)

Unnamed node (*Acrophoca* + *Homiphoca* + *Piscophoca* + "*Monachus*," *Mirounga* + *Lobodontini*): 55\*, 58\*, 78\*, 84, 96\* (1 to 2), 106\*, 134\*

Unnamed node (*Acrophoca* + *Homiphoca* + *Piscophoca*): -2, 36\*, 53\*, 64\* (3 to 2)

Unnamed node (*Homiphoca* + *Piscophoca*): 82, -119, 121\*

*Piscophoca*: 65\* (2 to 1)

*Homiphoca*: 3, 16, -91, -114

*Mirounga*: 16

"*Monachus*": -137

*Lobodontini*: 16\*, 36\*, 82\*, 84 (1 to 2), 96\* (2 to 1), 130\* (2 to 1), 131\*, -134

Phocinae: (*Erignathus* + *Cystophora* + Phocini): -2, 21, 44, 82\*, 83, -85, 88 (1 to 2), -89, -91, \*93, \*97, -100, -101, -103, -104, -105, -107, -108, 121, 130\* (2 to 1), 131\*

Unnamed node (*Cystophora* + Phocini): 18, 38, 43 (1 to 2), -56

*Cystophora*: 55\*, -93, 106\*

*Erignathus*: 16, -133, -137

Phocini: 111

Odobenidae: 17\* (1 to 2), 58\*, 93\*, 96\* (1 to 2), 99, 125

*Imagotaria*: 64\* (3 to 2), 97\*, -116, -120

Unnamed node (*Aivukus* + *Gomphotaria* + *Odobenus*): 55\*, 61, 62\*, 68\*, 78\*, 99 (1 to 2)

Unnamed node (*Gomphotaria* + *Odobenus*): 1\*, -3, 12\*

*Odobenus*: 3\* (0 to 2), \*65 (1 to 2)

*Gomphotaria*: 17\* (2 to 0), -37, -113